Biochronology and zoogeographic affinities of the Villafranchian faunas of Bulgaria and South Europe

Nikolai SPASSOV

Introduction. The Villafranchian fauna of Bulgaria

Until recently the Villafranchian in Bulgaria was scarcely studied. The only Villafranchian (Late Villanian) faunistic complex of a vertebrate fauna has been found in the cave Temnata Doupka (bore hole - IV) (POPOV, 1991). However, only Micromammalia have been reported there. Concerning Macromammalia, only some isolated and not precisely dated findings mostly of Proboscidea were registered up to the 90ies (SPASSOV, 1997b). In the 90ies some especially important Bulgarian localities of Villafranchian vertebrate fauna were studied - the Varshets and Slivnitsa ones (BOEV, 1996; POPOV & DELCHEV, 1997; SPASSOV, 1997a; 1998: SPASSOV & CREGUT-BONNOURE, 1999.). These investigations motivate an analysis of the Villafranchian in SE Europe. The continental Villafranchian fauna is a transitional one by its character. It reflects the considerable zoocoenological transformations and the radical change of the forms during the transition from the heat-loving (thermophilous) Neogene fauna to the cold-loving typical Pleistocene (Quaternary) fauna, The zoogeographic position of The Balkans in the zone of migrations between Europe, Asia and even Africa makes its fossil faunas of special interest: The study of the Villafranchian faunistic complexes on the Balkans is of a great significance for the elucidating of the origin and development of this fauna in Europe.

I. The first signs of the Ruscinian/Villafranchian transition in Bulgaria and the Balkans

The Musselievo locality: The first signs of the Ruscinian/Villafranchian transition are present in Bulgaria and the Balkans with the new locality of

Musselievo. The rich Micromammalia fauna indicates that the locality belongs to MNQ15 (POPOV & DELCHEV, 1997). The preliminary list of Macromammalia (det. N. Spassov) confirms this suggestion. The taxa determined up till now (even though all of them after scarce and fragmentary remains) are:

CARNIVORA: Vulpes sp., aff. Nyctereutes sp., Felidae indet. - large form (Dinofelis?); PERISSODACTYLA: cf. Stephanorhinus jeanvireti, Tapirus arvernensis, ARTIODACTYLA: Sus arvernensis minor, Cervus cf. pardinensis, cf. Procapreolus sp., aff. Gazella sp.

We could add ?*Lynx* sp. (V. Popov, Inst. of zoology, Bulg. Acad. Sci. - personal communication) and aff. *Macaca* sp. (1 molar) originally announced by V. Popov as *Dolychopithecus* (POPOV & DELCHEV 1997). Among the remains there are other taxa too, being currently studied.

Vulpes sp. from Musselievo must be the earliest fox found in Europe. The find comes to a sole P⁴ (Fig. 5). This tooth is considerably smaller than P⁴ of Eucyon adoxus. The tooth length, hardly reaching the lower limits of the individual variation of *V. alopecoides* from the European Villafranchian, but in the same time its width completely fits in (lab.L - 10.9; Ling. L - 11.6, W. max. - 5.8). The reason for that is the relatively well shaped and lingually protruding protocone of that otherwise slender tooth. The base of the parastyle slightly protrudes frontally as in *V. alopecoides* and in contrast to the recent *V. vulpes*, but we could not speak of an obvious rudiment of the parastyle as in the Chinese fox from the beginning of the Villafranchian *V. beihaiensis* (a find of ca. 3.3 - 3 Ma) (QIU & TEDFORD, 1990). The newly described - also from MNQ15 of Turkey (Calta) - *Vulpes galaticus* (GINSBURG, 1998) seems to be larger than the Muselievo find and its protocone does not protrude lingually.

After the composition of the macromammal fauna and the appearance of the faunistic complex of the megafauna the locality should most probably be placed in the second half of the MNQ15 zone. It is even rather possible that it is not much older than Vialette (France) and Triversa (Italy). Those localities aged 3.3 - 3.2 Ma are traditionally even to this day referred to the beginning of the Villafranchian (AZZAROLI, 1977; GLIOZZI et al. 1997), but according to some recent opinions (BONIFAY,1990; AZANZA et al., 1997) after their appearance they rather belong to the Final Ruscinian localities. Bearing in mind the strong presence of some typically forestal elements in those localities, such a suggestion seems reasonable. Both the micromammalian (POPOV & DELCHEV 1997; POPOV - in preparation), the macromammalian (mentioned here) faunas and the ornithofauna (BOEV, in press a &b) show the specific and even unique mixing of forestal and steppe elements. This probably indicates not only the presence of specific biotopes, but also starting climatic changes and a penetration of steppe elements into SE Europe by the second half - the end of the Ruscinian.

II. The biochronology of Varshets and Slivnitsa localities and the Middle and Late Villafranchian in Europe

II. 1. The Middle Villafranchian in Europe and biostratigraphic analysis of the fauna of Varshets

The Megafaunal List (Micromammalia) of the two localities (Table 1) allows their chronological orientating by the use of the available basic criteria of biochronologization: for example the well known zones for the Neogene and the Quaternary based on the Mammal faunas (i.e. zones MNQ) (GUERIN, 1982; 1990), and according to the faunistic associations (units) proposed by AZZAROLI (1977) for the Villafranchian in Europe.

The mammal megafauna of this locality demonstrates an evident similarity with localities typical for the MNQ17 zone, such as Saint-Vallier, La Puebla de Valverde (Spain), Chilhac (France) etc. After the conclusions on the morphological stages of some species, sites as Chilhac and Le Coupet were usually placed later than St. Vallier (DUVERNOIS & GUERIN, 1989). Mostly after geological considerations BOEUF (1997) puts, however, these localities before St. Vallier (see Fig. 1).

The St.-Vallier's fauna is among the best investigated Villafranchian mammal ones (VIRET, 1954; HEINTZ, 1970; MARTIN, 1971; DEBARD et al., 1994, etc.). Because of the various, abundant and well preserved material from this locality and of the detailed investigations carried there by a number of authors, the latter is appointed as the stratotype locality of the Middle Villafranchian and as the "*repere*" - type locality of the biozone MN 17 of Mein (= MNQ17 after Guerin's interpretation of the Neogene-Quaternary) (HEINTZ et al., 1974; MEIN, 1990; GUERIN, 1990).

The finalized recent faunistical List of the Mammals (after DEBARD et al., 1994 and with some taxonomical/nomenclature corrections of ours) includes the following forms:

RODENTIA: Mimomys pliocaenicus, Castor plicidens, Hystrix refossa; LAGOMORPHA: Oryctolagus lacosti, Ochotona sp.;

PRIMATES: Macaca sylvana;

CARNIVORA: Nyctereutes megamastoides vulpinus, Vulpes alopecoides, Baranogale helbingi antiqua, Pannonictis ardea (P. S. - included in the List as Enhydrictis ardea), Aonyx bravardi, Meles thorali, Ursus etruscus, Pliocrocuta perrieri (P. S. - included in the List as Pachycrocuta), Chasmaportetes (=Euryboas) lunensis, Lynx issiodorensis, Viretailurus schaubi, Acinonyx pardinensis, Homotherium crenatidens, Megantereon megantereon;

PROBOSCIDEA: Anancus arvernensis, Mammuthus meridionalis;

PERISSODACTYLA: Dicerorhinus etruscus etruscus, Equus stenonis vireti; ARTIODACTYLA: Sus strozzii, Croizetoceros ramosus medius, "Cervus" filisi

Table 1

Check-list of the large mammals from the Slivnitsa and Varshets localities (Bulgaria)

V - Varshets; S - Slivnitsa

Torra	Loc.
Taxa	LUC.
CARNIVORA	
Canidae	G
Canis ex gr. etruscus Major, 1877	s V
Vulpes alopecoides F. Major, 1877	v S
Vulpes cf. alopecoides	v V
Nyctereutes cf. tingi Tedford et Qiu, 1991	v
Ursidae	v
Ursus minimus D. de Chabriol et Bouillet, 1827 - Ursus etruscus Cuv., 1823	V
Mustelidae	17
Martes wenzensis Stach, 1959 - Martes vetus Kretzoi, 1942	V
Pannonictis ardea (Bravard, 1828)	V
Vormela petenyii Kretzoi, 1942	V
Baranogale balcanica nov. sp.	V
Meles thorali Viret, 1951	V + S
Lutrinae gen.	S
Hyaenidae	*7
Pliocrocuta perrieri (Croizet et Jobert, 1828)	V
Hyaenidae gen. (non P. brevirostris) Felidae	S
Lynx issiodorensis issiodorensis (Croizet et Jobert, 1828)	v
Panthera cf. gombaszoegensis (Kretzoi, 1938)	s
aff. Viretailurus schaubi (Viret, 1954)	v
Acinonyx pardinensis Croizef et Jobert, 1828	v
	s
Homotherium crenatidens (Fabrini, 1890)	5
ARTIODACTYLA	
Cervidae	v
cf. Cervus rhenanus Dubois (= C. philisi)	v S
Cervus rhenanus - Pseudodama nestii	v V
Eucladoceros senezensis cf. vireti Heintz, 1970 Eucladoceros cf. senezensis ? senezensis (Deperet, 1910)	S
Cervidae gen. et sp. indet.	v
Bovidae	v
Gazellospira cf. torticornis (Aymard, 1854)	S
Gazellospira sp.	v
Procamptoceras cf. brivatense Schaub, 1923	s
Gallogoral meneghinii (Rutimeyer, 1878)	s
	S
Pliotragus cf. ardeus (Deperet, 1883)	V
Megalovis aff. latifrons Schaub, 1923	
Megalovis sp.	S
Hemitragus nov. sp.	S
Ovis sp.	S
Bovidae gen. et sp. indet I	S
Bovidae gen. et sp. indet II	S
PERISSODACTYLA	
Equidae Equus stenonis vireti Prat, 1964	v
Equis stenonis Vient Prat, 1964 Eaus cf. stenonis Cocchi, 1867	s
	5

valiensis, Eucladoceros senezensis vireti, Gazella borbonica, Gazellospira torticornis, Gallogoral meneghini, Leptobos elatus merlae.

Very rich and well investigated is also the fauna of La Puebla de Valverde in Spain (GAUTIER & HEINTZ, 1974; KURTEN & CRUSAFONT, 1977; HEINTZ, 1978; AGUIRRE & MORALES, 1990). The List of the Macromammalia (after HEINTZ, 1978 and AGUIRRE & MORALES, 1990) includes:

PRIMATES: *Macaca* sp., *Papio* (= *Paradolichopithecus*) arvernensis (P.S. - nota mea N. S.: here maybe an earlier species is concerned in fact, see SZALAY & DELSON, 1979);

CARNIVORA: "Canis" sp. (P.S. erroneously mentioned in the List as C. cf. falconeri, see Spassov 1998; maybe an Eucyon is concerned in fact?), Vulpes alopecoides, Nyctereutes megamastoides, Ursus etruscus, Pliocrocuta perrieri, Chasmaportetes lunensis, Acinonyx pardinensis, Lynx issiodorensis, Panthera cf. schaubi (i.e. Vitretailurus cf. schaubi nota mea, N.S.), Megantereon megantereon, Felidae indet.;

PROBOSCIDEA: Mammuthus meridionalis;

PERISSODACTYLA: Dicerorhinus etruscus, Equus stenonis;

ARTIODACTYLA: Gazella borbonica, Gazellospira torticornis, cf. Gallogoral meneghinii, Croizetoceros ramosus pueblensis, Cervus philisi, Eucladoceros senezensis vireti.

Although the faunas of St.-Vallier and of P. de Valverde are quite similar, some distinctions between them could be found concerning the predominance of forest or steppe elements. In St. Vallier, the sylvatic elements are nearly as numerous as the steppe ones, what suggests the existence of steppes crossed by wood massives (DEBARD et al. 1994). In the P. de Valverde locality on the contrary, the steppe species are predominating, suggesting a more arid landscape (GAUTIER & HEINTZ, 1974). The absolute age of St. Vallier is estimated to 2 Ma (DEBARD et al., 1994). The geographic distance between St. - Vallier and La Puebla is not so large and the faunistic differences are probably not only biotopic. La Puebla is generally placed (after the evolution stage of some *Cervidae*) just earlier than that French locality. However, after the mantioned paleoecological data a more latter position - on the limit with the dray climate of the SCT10 could be supposed(Fig. 1). Such a statement could be reasonable if the specific zoocoenosis of the locality has not been resulted by a more southern local climate.

After the ecological interpretation of the landscape, The Varshets locality seems to be closer to the St.-Vallier one, rather than to the P. de Valverde (see next chapter). Two faunistic features give a reason to assume that Varshets (in the frames of MNQ17) represents a faunistic complex earlier than St.-Vallier (Fig. 1):

1. The find of *Gazellospira* sp. (more primitive than *G. torticornis*). Another, identical bone fragment with preserved diaphysis (large metatarsus dist. with more flat plantar surface than *Gazellospira* in general) was found by the author (undescribed material - coll. University of Lyon) in the Roccaneyra locality. The

faunal composition of this chronologically disputable French locality resembles the fauna of St.-Vallier, but with differently structured communities: species of open spaces are much better represented there. Now this locality is placed in the beginning, or in the first half of the Middle Villafranchian and of the MNQ17 zone. (After some authors - STEININGER et al., 1990, etc. - it should be placed even in the end of MNQ16). The calculation of its absolute age puts it between 2,35-2,0 Ma (BONIFAY, 1990, etc.), but, from the point of view of the faunal analysis, the first mentioned age seems to be more real.

2. The existence (see SPASSOV, 1997a) of Nyctereutes cf. tingi - a species lesser specialized than N. megamastoides and recently described from China (TEDFORD & QIU, 1991). This species existed in China up to the end of the Gauss chrone, i.e. up to the Early Villafranchian's end. N. tingi is noted recently also for the MNQ15 of Greece, in the Megalo Emvolon locality (KOUFOS, 1997). These two finds from the Balkans are the only finds known outside China so far (The Calta N. donnezani (GINSBURG, 1998) from the MNQ15 of Asia Minor is problematic). The species probably reached SE Europe, remaining there as a relict population even somewhal later than in C. Asia.

Those two finds put Varshets some earlier than St.-Vallier in the MNQ17 frames, most probably in the first half of the MNQ17 zone. This conclusion is supported by the data of the evolutionary stage of *Ursus* and *Martes* in Varshets. The Bulgarian locality seems to be approximately of the same age or most probably a little bit later than Roccaneyra, where the steppe faunistic element is better represented and where *Hipparion* is still existing as a relict genus (Fig. 1) (SPASSOV, 1997a; 1997b).

II. 2. The Late Villafranchian in Europe and biostratigraphic analysis of the fauna of Slivnitsa

The faunal differences between Varshets and Slivnitsa (Table 1) are based upon ecological and chronological reasons. Most conforming are some carnivorous species, which is connected with the greater adaptation ability of most carnivores.

The Biochronological position of Slivnitsa needs a discussion on some well known "repere"- type localities from Europe, such as Seneze and the localities from the Olivola Unit, which Slivnitsa is similar to (SPASSOV, 1995; 1997a; 1997b; 1998).

The position of Seneze locality. The total list of the Macromammalia in this rich and well explored locality appears as following (the list follows that of HEINTZ et al., 1974, with additions and corrections after the papers of MARTIN, 1973; EISENMANN, 1980; SZALAY & DELSON, 1979; DUVERNOIS & GUERIN, 1989, and BOEUF, 1997, with several corrections of mine concerning the synonimy):

PRIMATES: Paradolichopithecus arvernensis, Macaca cf. florentina;

CARNIVORA: Nyctereutes megamastoides, Vulpes alopecoides (?), Canis cf. arnensis (= Canis senezensis - see the chapter about Canis from Slivnitsa and the "Wolf event"), Ursus etruscus, Pliocrocuta perrieri, Chasmaportetes lunensis, Acinonyx pardinensis, Megantereon megantereon;

PROBOSCIDEA: Mammuthus (Archidiskodon) meridionalis,

PERISSODACTYLA: Equus stenonis "senezensis", Equus major (= E. bressanus), Dicerorhinus etruscus;

ARTIODACTYLA: Sus strozzii, Croizetocerus ramosus minor, Cervus philisi philisi, Eucladoceros senezensis senezensis, Cervalces (Libralces) gallicus, (?Gazella borbonica), Gazellospira torticornis, Gallogoral meneghinii, Pliotragus ardeus, Procamptoceras brivatense, Megalovis latifrons, Leptobos etruscus, Leptobos furtivus, "Ovis" sp.(about the latter species see somewhat below).

The stratigraphic position of Seneze is very controversial. Some faunal finds make several authors suggest there a mixt fauna or two Villafranchian levels in the locality (SCHAUB, 1944; V. EISENMANN, N.M.N.H. - Paris: personal communication). However, other detailed investigations lead to the opinion that the Seneze assemblage is homogenous; only the findings of "*Ovis*" and one of the Equus could possibly be refereed to an upper horizon (C. GUERIN, Univ.-Lyon.: person. comm.).

If we accept that the locality's fauna is homogenous, two possible main decisions regarding the age of the locality could be proposed:

Var. I. Final Pliocene age: This conception is supported by the biochronological analyses of the Italian authors (TORRE et al, 1992; GLIOZZI et al., 1997). The presence of Nyctereutes and the lack of Pachycrocuta brevirostris represent also faunistic arguments for such a chronological position (the lack of a species in the zoocoenosis and/or the taphocoenosis is not a direct proof for an environmental changes but it could be an important indication for it). Generally Seneze is related with the magnetostratigraphic event of Reunion. Some very recent interpretations place Reunion and Seneze earlier than 2.1 Ma (see in: GLIOZZI et al., 1997). This, however, does not seem logical from the point of view of the latest absolute age estimations of the St.-Vallier locality - 2 Ma (DEBARD et al., 1994), a locality which after its fauna is obviously earlier than Seneze. BAKSI (1993) notes that more than one Reunion Event is possible. Some other recent interpretations about the absolute dating show the following: the dating of the upper basalt layers situated just under the fossils in Seneze indicates an age of 2 Ma (end of Reunion). The fossil remains themselves should be a little bit later than that age - between Reunion and Olduvai (BOEUF, 1997).

Var. II. After another opinion Seneze should be placed in the very beginning of the Pleistocene or at least later than Olivola Unit (DUVERNOIS & GUERIN, 1989; BONIFAY, 1990; C. GUERIN - person. comm.). Such a chronological position - lather than Olivola unit could be supported partially by the presence of a horse (one of

the three species in the locality) close to the horse of Farneta (V. EISENMANN, pers. comm.). The above mentioned opinion concerning the Seneze biochronology could be related also with the placement of Tasso unit more close to the Middle Pleistocene boundary because of the appearance of *Hippopotamus* (C. GUERIN - pers. comm.). However the first appearance of this genus just in post-Olduvai time is possible especially having in mind the climathic stages - SCT 9 of ZUBAKOV & BORZENKOVA (1990) for the Tasso time (see the place of SCT9 - warming:- Fig. 1-2).

The Olivola unit. These localities as a whole, (and Slivnitsa as well) are characterized by the existence of lots of *Bovidae*, together with *Canis* and also *Panthera gombaszoegensis*. The faunal list of the Macromammalia of the Matassino includes following species (after TORRE et al., 1993):

CARNIVORA: Canis etruscus;

PROBOSCIDEA: Mammuthus (Archidiskodon) meridionalis;

PERISSODACTYLA: Equus stenonis, Dicerorhinus etruscus (found in the neighbourhood);

ARTIODACTYLA: Sus strozzii, Pseudodama nestii, Eucladoceros dicranios, Leptobos etruscus.

The Faunal list of Olivola loc. is as follows (ALBERDI et al., 1998):

CARNIVORA: Canis etruscus, Ursus etruscus, Enhydrictis ardea (i.e. Panonnictis ardea - nota N. S.), Chasmaportetes lunensis, Pachycrocuta brevirostris, Homotherium crenatidens - H. ex. gr. latidens, Megantereon cultridens (i.e. M. megantereon - nota N.S.),

?Acinonyx pardinensis, Lynx issiodorensis, Panthera gombaszoegensis PROBOSCIDEA: Mammutus meridionalis meridionalis

PERISSODACTYLA: Stephanorhinus etruscus, Equus stenonis

ARTIODACTYLA: Sus strozzii, Eucladoceros dicranius olivolanus, Pseudodama nestii, Leptobos etruscus, Leptobos ex gr. merlae - L. furtivus, Gallogoral meneghinii, Procamptoceras brivatense

This unit is generally related with the beginning of the Late Villafranchian (AZZAROLI, 1983; TORRE et al., 1992; 1996). Up to now the sites of Olivola Unit were placed just in the beginning of the Pleistocene, but recently this unit was placed just at the end of the Pliocene or on the Plio-Pleistocene boundary (TORRE et al., 1993; 1996; GLIOZZI et al., 1997). According to the decisions of the XII INQUA Congress, the Neogene/Quaternary boundary should be placed a little later than the end of the Olduvai subchrone in the Vrica marine section. (Italy). The end of Olduvai is calculated at 1.65 Ma but recently at 1.78 (BAKSI, 1993; TORRE et al., 1996) and the beginning of the pleistocene at ca. 1.76 (BAKSI, 1993). Some modern investigations on the palaeomagnetism suggest that the boundary between the Middle- and the Late Villafranchian in Europe marked after correlation of the sediments from the Matassino locality in Italy (as a marker of the Late Villafranchian Beginning, being a typical locality from the Olivola unit) is

situated in the upper portion of the Olduvai subchrone (Upper Pliocene), or immediately after its end (the Beginning of Pleistocene) (TORRE et al., 1993; TORRE et al., 1996) This locality could be referred to the End of Olivola unit or to the transition between Olivola and Tasso units (GLIOZZI et al., 1997).

Faunal and biochronological comparisons with Slivnitsa. Especially remarkable is the similarity of Slivnitsa megafauna (Table 1) with the fauna of Seneze (SPASSOV, 1997a; 1997b; 1998) The fauna of artiodactyls from Slivnitsa (for Bovidae determination - see SPASSOV & CREGUT-BONNOURE, 1999), as well as the presence of *Canis* and *Panthera*, suggests similarities with the localities from the Plio-Pleistocene boundary or the very Beginning of the Pleistocene - e.g. Olivola, Matassino (Olivola "Unit"). Therefore P. brevirostris existing for the first time in Europe in Olivola Unit is still not present in Slivnitsa, as it was mentioned above. At the same time tooth morphotypes of the Microtinae correspond to a stage of evolution which must be looked for close by the Plio-Pleistocene boundary, but earlier than this boundary: 1. Absence of *Allophaiomys pliocaenicus*, *M. deucalion* and *Lagurus arankae*, 2. Presence of an morphotype of *Mimomys tornensis* corresponding to a stage of evolution connected with the Plio-Pleistocene boundary but more exactly with the time before this boundary (V. Popov: Zool. Inst., Sofia - pers. communication).

The prevailing hoofed mammals of open spaces (xerophytisation) suggest also that the fauna of Slivnitsa locality should have existed still before the Olduvaian warming, i.e. before the date 1.9 Ma and during the cooling known from Georgia as Meria (2,0-1,82/1,86 Ma ago) (ZUBAKOV & BORZENKOVA, 1990).

So the Micromammalian data and the characteristics of the Macromammalian megafauna of Slivnitsa (predominance of *Bovidae* on *Cervidae*, presence of the genera of Panthera and Canis, presence of Hyaenidae but not of Pachycrocuta brevirostris) enable the establishing of rather narrow chronological boundaries of the time the locality's fauna should be referred to - just at the end of Pliocene, between the localities from the end of the MNQ17 (St.-Vallier, Chilhac) and those from the Plio-Pleistocene boundary (Olivola "Unit") (Fig. 1-2). Thus, the Slivnitsa locality should be placed into the Costa St. Giacomo unit and in SCT10. The zone MNQ18 should have started after 2,0 Ma. - in the end of Pliocene and not in the beginning of Pleistocene (see below). Slivnitsa must be placed at the beginning of this zone too (Fig. 1-2). If a nearly equal age of Slivnitsa and Seneze is accepted (in case of the pre-Olduvai interpretation of the Seneze age - see above), Slivnitsa could be somewhat older of both however; An old Hemitragus - Hemitragus sp.nov., is present in Slivnitsa. This is a species whose remains closely resemble the finds of that Genus in Villany 3 (SPASSOV & CREGUT-BONNOURE 1999). Villany 3 is referred to MNQ17, but it evidently envelopes a longer period (see below), so that several finds, including Hemitragus, correspond to the level of MNQ18's beginning and to C. S. Giacomo unit (op. cit.).

Several faunal resemblances (see, Canis, Panthera and the bovids) exist between Slivnitsa and Gerakarou (Greece). But Gerakarou could be something later in age than Slivnitsa (see next chapter), where *P. brevirostris* is not present in the fossil sample (about 1000 bones). (Fig. 2).

II. 3. Biochronology of the Villafranchian in Europe. Specifying, addition and correlation of the biochronologic criteria concerning the Middle and Late Villafranchian

An important circumstance by modern biozonation is the constant accumulation of new data about the composition and characteristics of the fauna, resulting in an outdating of the biochronologic criteria. Repeated suggestions were made recently to update the subdivisions of Villafranchian (KOSTOPOULOS & KOUFOS, 1995; KOSTOPOULOS, 1996), Also, there are new efforts to update the chronology of Plio-Pleistocene mammal faunas (AZANZA et al., 1997). The biochronologic division of the West Mediterranean Plio-Pleistocene by those authors was based on multivariate analysis of faunal similarity and was an attempt to objectively define the boundaries of biotic events in the evolution of mammal faunistic associations in time. The general frameworks set by this analysis agree more or less with the existing concepts. Distinctions come when comparing the basic faunistic units of this new biochronologic scheme with the generally used Mammal units - those of MEIN 1975; 1990 (with the contribution made by GUERIN 1982; 1990), those of the Italian school (AZZAROLI, 1977, TORRE et al., 1992 etc.), and those of AGUSTI et al. (1987), Although the faunistic microunits C and D by AZANZA et al. (1997) reflect well the boundaries and stages of the main current faunistic events, they are not precise enough to clarify the details in the faunal evolution process. So, merging the Italian school's Olivola and Tasso units, if reasonable from the point of view of following the main stages of the faunas evolution, permits no detailed tracing of the successions. The difference between Olivola and Tasso after the latest existing species or genera (Chasmaportetes - Olivola), or after the first appearance by a number of Macromammalia ("Leptobos" vallisarni, Hippopotamus, Canis falconeri etc. - Tasso unit), is obvious enough (see AZZAROLI, 1983; TORRE et al., 1992).

Thus, despite this modern approach to the biochronology of mammal faunas, the "old" and more detailed "MNQ zones" and "faunal units" don't lose their meaning. Contrary to some opinions, those two different systems of biochronology could be successfully correlated. A complex method (MNQ zones/Faunal units) of Plio-Pleistocene biochronology would turn helpful for a more detailed study of Villafranchian successions and also for an after division of the Villafranchian and setting the boundaries of its stages.

However, the effective use of the two methods is possible only after updating the definitions and boundaries of the MNQ zones and the faunal units concerning the Plio-Pleistocene having in mind the recent faunal data.

An example of the necessity of updating could be given with the Villafranchian MNQ-zones 17 - 19. These zones are of a special importance as far as they are connected with the evaluation of the faunal events on the Pliocene-Pleistocene boundary.

1. The definition of zone MNQ19 (GUERIN, 1982; 1990) includes, for example, the appearance of *Canis etruscus*. This appearance is connected after TORRE et al, (1992) with the localities from the "Olivola unit", placed recently near the Plio-Pleistocene boundary (the age of the localities Olivola-Matassino has been estimated recently at ca. 1.8 Ma., see TORRE, et al., 1996, GLIOZZI et al., 1997) (Fig. 1). We see, however, that this species enters Europe probably earlier, still in Slivnitsa (SPASSOV, 1998). In fact, what is important here is not the appearance of this exact species, but something more - the so called "*Canis event*": the penetration in Europe of the wolf-like *Canis* (AZZAROLI, 1983; TURNER, 1992; TORRE et al., 1992; ROOK & TORRE, 1996). That event is obviously earlier than Olivola (and Seneze?) after the Slivnitsa data and should be connected with the final Pliocene.

C. "senezensis", found in Seneze, which has large diastemae between the premolars could be referred to *C. arnensis*, resembling the latter also after its size. Indeed, *C. arnensis* was not found until recently earlier than Tasso (Italy), but KOUFOS (1987) has announced it from Gerakarou (Greece). The age of the Gerakarou locality, where Pachycrocuta brevirostris is present as well, is probably at the boundary between Seneze and Olivola units (see below). All that suggests that the appearance of C. etruscus and the "Canis event" in general should now be placed in the definition of the MNQ18 zone.

2. At the same time, the definition of the MNQ18 includes also the appearance of Allophaiomys pliocaenicus, Procamptoceras, Megalovis. Now we know that A. pliocaenicus invaded Europe ca. 1,6 Ma ago. This is a time considerably later than the time of the appearance of C. etruscus and Caniss.str. in general, as well as the time of appearance of Procamptoceras and Megalovis after the recent data. Procamtoceras is already established also in MNQ17 (DUVERNOIS & GUERIN, 1989), and, affer the investigations in Varshets, Megalovis was inhabit Europe also since MNQ17 (SPASSOV & CREGUT-BONNOURE, 1999; SPASSOV, 1997a).

The fauna characteristic for Costa St. Giacomo Unit of GLIOZZI et al. (1997) (="Seneze" faunal unit of TORRE et al.,1992) is a Pliocene (Final Pliocene) one. Nevertheless, the "physiognomic" differences between the faunas of the "St.-Vallier (including Varshets) Unit" and of the "C. st. Giacomo Unit" (including Slivnitsa) are greater than the differences between the latter faunal unit and the faunas from Late Pliocene boundary and the beginning of Pleistocene (Olivola - Matassino). The aridification, having taken place in the period between St.-Vallier/Varshets and C. St. Giacomo/Slivnitsa, has resulted in the above mentioned intensive penetration of *Bovidae (Caprinae)* and of the open spaces carnivores, such as the modern wolf-like *Canis* ex gr. *etruscus* and C.

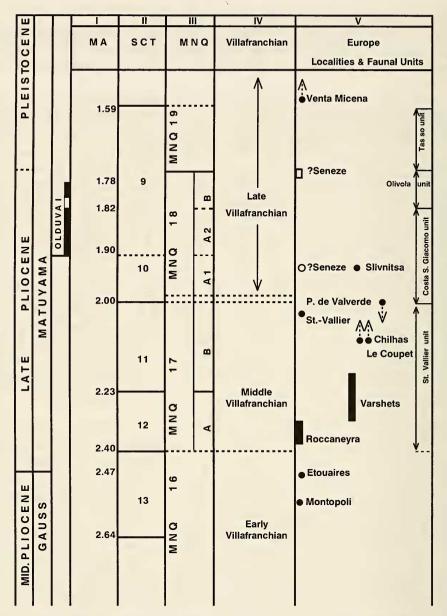


Fig. 1. - Biochronology of the Villafranchian localities of W. Europe. Correlation of the climatic and faunal events (after Spassov, 1997-a; 1997b; 1997c, with additions and modifications): Column I - Geochronology, Absolute age and magnetostrarigraphy; Column II - Climatic stratigrafic subdivision (superclimathemes - SCT) of Zubakov & Borzenkova with minor modifications. Column III - Mammalian biozones of Guerin; Column IV - The Villafranchian subdivision; Column V - Major localities and the Faunal Units of Azzaroli - Gliozzi et al. 1997 (see the text). For the controversal position of Seneze - see the text.

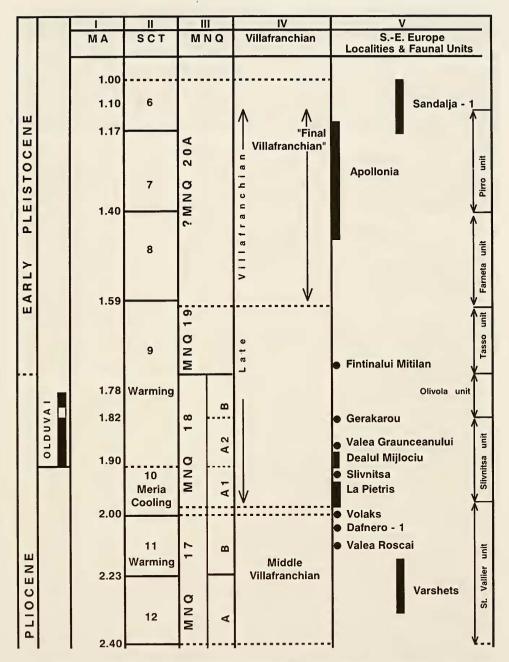


Fig. 2. Biochronology of the Villafranchian localities of S-E. Europe. Correlation of the climatic and faunal events (after Spassov, 1998, with additions and modifications. (The explanations as in Fig. 1).

P.S. The biochronologic positions of localities as Roccaneyra, Varshets, La Pietris, D. Milociu, Apollonia & Sandalja 1 are presented within probable ranges.

"senezensis" and Panthera gombaszoegensis. The general outlook of this more "steppe" fauna becomes just confirmed in the period between C. St. giacomo and Gerakarou/Olivola by the appearance of some species (e.g. of Pachycrocuta brevirostris). (Indeed, P. brevirostris is found in the Hapry faunal Complex of the Sea of Azov region - South Russia, whose age is referred to the beginning of MNQ17. Its presence there, however, could by a result of: 1. The direct contact with Asia; 2. The possible presence of younger layers (SOTNIKOVA et al., 1998)).

Seneze remaining the type locality of MNQ18 (GUERIN, 1982) we can attach to this zone also the localities from the Plio-Pleistocene boudary - such as Olivola creating the subzone of MNQ18-b (appearance of *P. brevirostris* - see MASINI & TORRE, 1990) (Fig. 1). In the MNQ18-a1 we could place the Pre-Olduvai localities, with their physiognomy determined by species adapted to a more arid environment. In the MNQ18-a2 could be placed the Pre-Olivola localities (see Fig. 1-2) corresponding to the Olduvai subchrone, with a fauna requiring a more humid climate again. As a result, we can correlate the "Costa St. Giacomo unit" of Italian school with the first phase of Guerin's MNQ18 (=MNQ18a of this paper). Thus the MNQ18a (=C. St. Giacomo unit) would include a drier initial period - MNQ18-a1 (=SCT10 of Zubakov et Borzenkova - cooling) and a more humid final period - MNQ18-a2 (=Olduvai episode, =SCT9 firs phase - warming). (maybe not only the MNQ-zones but also some of the boundaries of the SCT-zones - e.g. SCT9's boundaries - need to be updated).

The opinion that the Late Villafranchian starts from the very beginning of the Pleistocene sounds plausible and is broadly accepted (MASINI & TORRE, 1990). It seems although that it is not exactly the case. Several facts show that the beginning of some typically Late Villafranchian phenomena have started yet in the End of Pliocene. Indeed the considerations mentioned above on Slivnitsa and Gerakarou fauna permit some new statements concerning the faunal changes to be suggested: faunal events usually considered typical for the beginning of Pleistocene in Europe (BONIFAY, 1990; TURNER, 1992) start in fact as early as the end of the Pliocene, especially in the eastern regions of the continent. Such phenomena are, for instance, the obvious development of the Bovidae (Caprinae) faunas and their prevalence over *Cervidae*, as well as the migration from the East (S-East) of the Panthera and Canis genera on the continent (see below). The find of Canis in Slivnitsa gives the explanation of the possible Early Pliocene appearance of Canis s. str. in the Seneze locality and could be an argument supporting the statement that the faunal composition in this French locality is rather homogenous. The beginning of the Late Villafranchian could be placed not in the Pleistocene's beginning but in the end of the Pliocene (zone MNQ18a = C. St. Giacomo unit, with localities like Slivnitsa) (Fig. 1-2).

II. 4. The problem of the correlation of the Western and Eastern European Villafranchian and biochronology of the localities from the adjacent territories

It was already noted that there is a logical tendency to correlate strtigraphically the biocomplexes in Eastern and South Eastern Europe and even in Central Asia with those earlier defined in W-Europe by using the same biostratigraphic criteria. The use of locally created criteria over much vaster territories, however, might cause some mistakes. Also disputable are the various methods of biozonating created (see the analysis in GUERIN, 1990). Some of the main problems of biozonating concern the temps and synchronization of the variability of the faunas, as well as the related question of the zoogeographic particularities of the local faunas.

We have to note that the rate of faunal changes is different with:

1. occupation of new environmental territories;

2. migrations and spreading of the faunas over new territories which propose the same or similar living conditions. The latter are usually at a specific or subspecific level (SPASSOV, 1997 c).

Casus 1. The occupation of new territories with an environment different from that typical for the taxa takes place in global natural changes associated with a considerable growing of certain biomes, or even with a creation of new ones. The settlement of new territories in such cases is based on pre-adaptation and is connected with an evolution of the taxa in time (usually on supraspecific level). Such a penetration into the new environment cannot happen instantly and is usually connected with new aromorphic accomodations and an impetus to the morphologic evolution of the groups. Such is the case, for example, with the aridification of N-America and C. Asia starting in the end of Eocene and actively continuing during the Oligocene. Those changes have given an impetus to the development of a number of "cursorial" *Tapiroidea* and *Rhinocerotoidea*, invading into the savanna from a forestal environment. Such type of distribution is slow enough and well detected by the geological annals.

Casus 2. Such distributions, associated mostly with the spacial adaptive radiation, usually do not result in evolutionary changes or changes on a supraspecific level. In this case it is almost not necessary for the species and faunas to accomodate towards the new living conditions, so in fact they simply enlarge their areals. This happens with forest species when a new deforestation has taken place, or with steppe species after an aridification of the climate or after the disappearance of a geographic barrier (e.g. formation of landbridge between two mainlands separated by water). In this case the distribution is rather fast - in fact instant from the point of view of geologic events (VANGENHEIM, 1977; FLYNN et al., 1984). The "dispersal events" of the Villafranchian faunas over the territories of today's Palaearctics should be referred to that case. Thus, the use of the zonation criteria of the Neogene-Quaternary, including the W-Europe Villafranchian for the whole continent and even for still vaster territories, is possible. However, the following should be had in mind:

Considerable differences are possible when comparing distant territories because of: 1. Existence of local faunas; 2. Penetration of certain species in the Eastern or Southern regions of Europe only (not so rapid dispersal of certain species, especially rodents is also rather possible. Such kind of relatively slow invasion could be accompanied by an asynchrony, if even slight, in the existence of the same species in W and E. Europe); 3. Retreat of the faunas and their relict existence in certain places long after their disappearance in vast territories.

Examples of such differences are numerous. So in the recent fauna of S-E Europe, Mesocricetus newtoni, Cricetulus migratorius, Talpa levantis, Mustela eversmanni, Vormela peregusna etc., existed during the whole Holocene, without penetrating to the West, New data shows (Kostopoulos, 1996;1998; Kostopoulos - in press) that the Villafranchian *Bovidae* fauna of Greece includes forms known particularly from the Circumpontic zone and Fore Asia, but not from the other regions of Europe: The *Cervidae* species from the Late Villafranchian of Italy are taxonomically quite different from those of Spain and France (see HEINTZ, 1970; AZZAROLI, 1983); Nuctereutes disappears in Europe as early as the end of Pliocene or the Pliocene/Pleistocene boundary . At the same time, in neighbouring to Europe palaearctic territories such as Palestine, this genus exists up to the End of Pleistocene (today it exist in natural conditions only in the Ussuri region); Megantereon also disappears in most of the territory of Europe (as already noted) as early as the very Beginning of the Pleistocene However, (see above) this genus survived in the Mediterraneum - Apollonia, Greece and Farneta to Pirro unit, Italy, Spain (TURNER, 1992; KOUFOS et al., 1995; GLIOZZI et al., 1997) - almost up to the End of the Early Pleistocene (the End of Late Villafranchian). The genus survived in Asia probably to the beginning of the Middle Pleistocene (WERDELIN & TURNER, 1996). Similar examples are also the existence of the lion in the Holocene only in SE-Europe, as well as the retreat of the leopard from Europe, and its surviving in the Holocene of the continent only in Caucasus.

II. 5. The biochronology of the Villafranchian localities in South-Eastern Europe

The problem of precise biochronology of Villafranchian in SE-Europe could be elucidated by comparison of the faunas existing there with those of the well known Central, and above all, West European localities. The reason is, the biostratigraphical criteria have been created namely on the base of their relatively high level of investigation in those regions. Some views concerning the biostratigraphy of some of the principal localities of W-European Villafranchian have been cited above.

Concerning the analysis of some of the localities in SE-Europe it is worth discussing the biostratigraphy of the well known Central European Villafranchian localities near Villany.

Villany 3-5, Hungary

The Plio-Pleistocene localities near Villany became famous all over the world thanks to the meticulous and rather contributive investigations carried out by a number of researchers (KORMOS, 1937; KRETZOI, 1956; JANOSSY, 1986). It is not accidental that the biostratigraphic concept "Villanian" is broadly used in many investigations as an equivalent of "Villafranchian". The stratigraphic position of the localities Villany-3 and Villany-5 is of certain importance for the present study. These two localities are practically equal in age, the second one maybe a little bit closer to the present time - see JANOSSY (1986), and some authors (MONTUIRE, 1994) estimate the age of Villany-5 at ca. 1,8 Ma. The modern faunistic lists of these localities are presented by JANNOSY (1986). The first of them - Villany-3 (= Villany-Kalkberg-Nord) is the richer one. After the broadly accepted opinion, its fauna belongs to the St.-Vallier Unit - zone MN17 of Mein (BRUJIN et al., 1992)p i.e. - to the Middle Villafranchian. It should be noted, however, that this zone in fact includes the MNQ17-18 zones in Guerin's interpretation, i.e. Late Pliocene up to its end (incl. the beginning of the late Villafranchian). Here we could place the Seneze unit, too, as it was already said. A proper question is if Villany-3 is limited by St.-Vallier unit, or concerns later faunal events as the Seneze unit (MNQ18 sensu Guerin), i.e. MNQ 18-a after the biozonation suggested in this work.

JANNOSY (1986) does not close Villany-3 in narrow frames and places it chronologically in the time between 2 and 1.5 Ma ago. Supporting that suggestion of JANOSSY (op.cit.), RADULESCO & SAMSON (1990) also note that the fossil bearing layers in Villany 3 are probably corresponding to a rather long period of time, with more than one faunal associations included there. The rather complicated geology of that karst locality appears to confirm such an opinion. Indeed, a number of forms listed in the locality - "Leo cf. gombaszoegensis", "Canis mosbachensis" (= C. etruscus), Vulpes (?) praecorsac, etc. - probably suggest an age not earlier, and maybe even somewhat later than Seneze and Slivnitsa (see corresponding Chapter above for more detailed information about the migrations of Canis s.str. and P. gombaszoegensis). The teeth of Hemitragus from Villany (Villany 3? - see JANOSSY, 1986: Hemitragus cf. bonali), kept in the old collections, are identical with the teeth from Slivnitsa (SPASSOV & CREGUT-BONNOURE (1999)). Probably we have there fossils of similar age/taxon, which could be connected with the migrations from the East during the cooling in the superclimatheme SCT10 of Zubakov et Borzenkova (see Fig. 2).

Southeasthern Europe

Romania: The Villafranchian fauna from the Oltet valley (Oltenia)

Some of the most interesting Villafranchian localities in Romania are concentrated in the regions of Tetoiu and Irimesti, the Oltet valley, and represent a successive Villafranchian fauna whose biostratigraphic state has been precisely analyzed by RADULESCO & SAMSON (1990; 1995). If comparing the Oltet sites with Varshets and Slivnitsa and having in mind the biostratigraphy discussed above, the localities from the lower horizon of Tetoiu and from the middle horizon of Tetoiu and Irimesti are of a special interest (Fig. 2).

RADULESCO & SAMSON (1990) conclude that the lower horizon could be correlated with the upper section of the MN17 zone of Mein (the Saint-Vallier zone). We have to stress again, however, that the MN17 zone includes both MNQ17 + MNQ18 zones (sensu Guerin). Or, the MN17 zone includes both the St.-Vallier unit and localities from the very End of Pliocene - later than St.-Vallier unit and with different faunal features: the Seneze unit (MNQ18-a in our interpretation) (Fig 1-2). The statement of RADULESCO & SAMSON (1990) could finally be interpreted as follows: the Lower Villafranchian horizon in the Oltet valley probably includes the End of MNQ17 and the localities later from St.-Vallier (the final phase of the Pliocene). We could also accept that conclusion. The latter could be confirmed and specified by comparing those Oltenian sites with Varshets and Slivnitsa having in mind our concept of the MNQ18 zone.

A. Lower horizon (Tetoiu region). The stratigraphy of the lower horizon of Tetoiu reveals the following succession of the localities with Villafranchian mammal fauna (see RADULESCO & SAMSON, 1990): Valea Roscai (the earliest one); La Pietris; Valea Graunceanului.

Most probably, Valea Roscai is approximatively corresponding to the level of the St.-Vallier locality. *M. (Archidiskodon) meridionalis* shows there some primitive teeth features (RADULESCO & SAMSON, op. cit.).

The later locality from that horizon - LA PIETRIS - shows the presence of several Villafranchian forms which disappear in Europe before the beginning of Pleistocene - *Nyctereutes megamastoides*. We must therefore accept that the locality is earlier than the Olivola unit, where the raccoon-dog has already disappeared. As it was already noted, the beginning of that biochronologic unit is situated in the very beginning of Pleistocene or most probably at the very end of Pliocene(i.e. at the Plio-Pleistocene boundary). *Pliotragus ardeus* is present in La Pietris, and horses prevail over deer - an indication of a more arid landscape. All these facts and especially the last one give reason an age similar to that of La Puebla to be proposed; i.e. the same age as that of the Mid/Late Villafranchian boundary (the SCT11/SCT10 boundary), or more probably, that of Slivnitsa - SCT10 (= MNQ18-a) (Fig. 2).

VALEA GRAUNCEANULUI. The Villafranchian raccoon-dog is still present here which shows that the locality is still a Pliocene one. The fauna of the locality includes also Pliotragues ardeus and Papio (Paradolichopithecus) arvernensis *aeticus.* It is worth noting that the co-existence of these two forms is typical for MNQ18-a (sensu the biostratigraphy proposed in this study) (i.e. the Costa St. Giacomo unit), However, Valea Graunceanului seems to be a locality later than Slivnitsa (a presumption made also by RADULESCO & SAMSON, 1990 concerning Seneze, in the pre-Olduvai understanding of the age of this site). Thus V. Graunceanului appears to be later than MNQ18-a1 due to following reasons: the deer prevail over the other hoofed mammals, and, at the same time, *Castor* is also presented there. This not only indicates biotopes more humid and forestal than those of La Pietris, but also a biostratigraphic position later than La Pietris. Valea Graunceanului should be placed within the frames of the Olduvai episode. We could separate it in MNQ18-a2, an age corresponding to the age of the superclimatheme SCT9 of Zubakov et Borzenkova. This superclimatheme differs from SCT10 by a new warming (Fig. 2).

B. Middle horizon (regions of Tetoiu and Irimesti). The localities from this horizon (e.g. Fintinalui Mitilan - Fig. 2) show some faunistic elements which have appeared during the Seneze unit (*Cervalces gallicus*), but they are obviously later (probably - Early Pleistocene) because of the presence of *Pachicrocuta brevirostris* and *Trogontherium boisvilletti*. After RADULESCO & SAMSON (1990) these localities are later than Olivola too and of equal age with Tasso due to the absence of *Anancus*. Indeed, such a conclusion appears to be the most probable but recently the last Anancus (from Costa S. Giacomo) is placed not in Olivola F.U. but something earlier. It is possible also that in the East European habitats with more steppe conditions this species could be already replaced by the *Elephantidae*. Another explanation of the lack of *Anancus* could be its rarity in this period, i.e. the lesser probability to be found: only 3-4 species of Macromammalia have been discovered in each of these two Romanian localities. With this note, we could suggest an approximate age of the localities from the Middle horizon - from Olivola to Tasso unit.

The republic of Croatia:

THE LOCALITY OF SANDALJA I. The locality of Villafranchian mammal fauna was investigated by MALEZ (1975), who evaluates the latter as being typical for the Middle and Late Villafranchian. He also suggests that the fauna there should belong to the earliest Pleistocene. From the viewpoint of the current data and notions we could define the general appearance of the faunal complex as Late to Final Villafranchian, and most probably, the end of the Early Pleistocene (i.e. Post MNQ18a). This suggestion is determined by the presence of such forms as *Canis etruscus, Oryctolagus, Leptobos* and "*Dama*" *nestii.* The species determination of *Leptobos* as *L.* "stenometopon", i.e. *L. elatus* should be revised because of the modern conception of this genus taxonomy, as far as this form is relatively early and does not correspond to the Final Villafranchian appearance of the locality as a whole. Judging from the frequent appearance of *E. stenonis* and *Leptobos* on the one hand, and of *Sus strozzii*, *Ursus* and *Cervidae* on the other, the existence of a forest-steppe landscape and a moderate, relatively mild climate could be supposed (with existence of *Macaca, Oryctolagus, "Dama " nestii, Francolinus*).

Similar to Dealui Mijlociu in Romania, the locality of Sandalja draws the attention with the remains of very ancient *Homo* - one incisor and a rather primitive stone tool of the "chopper" type. Due to that, the precision of that locality's dating is of a special significance.

A certain problem by the site dating is caused by the remains of the Ursus genus there. On the one hand, the simultaneous existence of three species - U. etruscus, "U. mediterraneus" (i.e. U. gr. minimus - tibetanus) and U. cf. deningeri - is dubious. The latter form (determined after one tooth fragment), on the other hand, is a species appearing not earlier than the very Beginning of Middle Pleistocene (ca. one million years ago - see in MAZZA & RUSTIONI, 1994). An infiltration of later material in a locality of Villafranchian fossils could be supposed, but there are no proofs at all for such an assumption at the moment, all the more that the fauna there appears (with the exception of U. cf. deningeri) homogeneous and of same age. Having in mind the insufficiency of this find, a certain subjectivity in its determination cannot be excluded (note also the uncertain determination - U. "cf." deningeri).

Nevertheless, the discussed taxonomic situation concerning the Ursus Genus, gives reason for a motivated suggestion from the point of view of the newest taxonomic analyses. The discovery of bear remains allowing the differentiation of the three forms cited above resembles the situation of Vallonnet, France (age 0.98-091 Ma,), and that of Pirro (Italy), with a probable age more than one Ma, (included in the Farnetta unit, after TORRE et al., 1992 or in the new "Pirro" unit after GLIOZZI et al., 1997), The bears from Vallonet show, after MAZZA & RUSTIONI (1994), mixed features of both U. denningeri and U. arctos (s. lato). These authors, at the same time, quote the fact that other researchers see there a presence also of *U. etruscus* - a species which should have disappeared earlier. The bear in Vallonet in fact shows a transitive state of evolution. The bear remains in Pirro also show some similarity with U. etruscus, but also a greater similarity with U. arctos (s. lato) (MAZZA & RUSTIONI, 1994). The distinction of "three" different forms in Sandalja I could quite probably be an indication of a similar stage of evolution. This circumstance, considered in the context of the faunal complex as a whole, makes possible to give this Croatian locality a likely age of approx, 1.2-1.0 Ma, and more exactly, somewhat more than one million years cf. Pirro unit (sensu GLIOZZI et al., 1997).

Greece:

A considerable number of localities of Villafranchian age have recently become known in Greece. Here we shall discuss some of the main localities from the Greek part of Macedonia (N-Greece), which are directly connected with the question about the Varshets and the Slivnitsa age, or are especially well known and discussed.

DAFNERO-1. The first report about this locality was recently published by KOUFOS et al. (1991). In this preliminary description the authors estimate its age as Middle-Late Villafranchian. Later Koufos and Kostopoulos specified the status of Dafnero-1 in a number of papers (KOUFOS, 1993; KOUFOS & KOSTOPOULOS, 1993; 1997; KOSTOPOULOS & KOUFOS 1994; KOSTOPOULOS, 1996). They placed it in the MNQ17 zone (= St.-Vallier unit) on the base of the similarity of the carnivores and, above all, of the horse and some Artiodactyla from the Greek locality with those from La Puebla, St.-Vallier and some other localities from that zone.

The giraffe Mitilanotherium (= Macedonitherium) known from Greece. Romania, Turkey and Tadjikistan, is one of the interesting faunal peculiarities of that Greek locality. Greece and Romania are so far the only European countries whose fauna contains with certainty giraffes from such a late time - the Villafranchian. Evidently, by the end of Pliocene those forms were typical for SE-Europe as an Asian element, because of the strongly thinned forestal vegetation of the "Tree-Savanna" type. RADULESCO & SAMSON (1990) see a great similarity and even a probable identity between the Mitilanotherium described from Romania, and the Macedonitherium from Greece. That opinion was confirmed by KOSTOPOULOS (1996), who considers Macedonitherium a junior synonym of Mitilanotherium. In Asia the Genus is known from the Middle Villafranchian of Guliazi and Kuruksay (Kostopoulos, 1996). The Romanian Mitilanotherium inexpectatum seemingly occurs in the time, defined by the zones MNQ18 and 19, as noted above. It is possible however, that Mitilanotherium martini from Greece is earlier, existing in the End of MNQ17 and probably surviving up to the MNQ18 (in Libakos, Greece, it is found together with Canis: KOUFOS & KOSTOPOULOS, 1993). It should also be noted that Nyctereutes megamastoides from Dafnero-1 is quite different from the Varshets one. At the same time, it differs also from the form known from St.-Vallier and La Puebla de Valverde - much more omnivorous, i.e. more evolved regarding the main tendency for that genus. If the form from Greece and that from France/Spain lived simultaneously, then what we are dealing with here are clear geographic (subspecific) differences in the dimensions and the frequency of appearance of the different teeth morphotypes.

Having in mind those features of the Dafnero-1 fauna we could place it somewhat later than Varshets, i.e. in the second half (the end?) of the MNQ17 zone, which actually confirms the pinion of the Greek researchers.

VOLAKS (VOLAKAS). The locality was described as early as the 60s as an Early Pleistocene (Villafranchian) one (SICKENBERG, 1968) and is broadly known now. The species mentioned by different authors are typical for the Middle and the first part of the Late Villafranchian (MNQ17-MNQ18): Vulpes sp., Nuctereutes megamastoides, Megantereon megantereon, Lynx issiodorensis, Mitilanotherium martinii Eucladoceros senezensis, "Cervus" philisi, Croizetoceros ramosus, cf. ? Leptobos, Gazellospira cf. torticornis, Gallogoral meneghinii sickenbergii, Gazella sp., Equus stenonis aff, vireti (in our opinion, the upper premolar -P4 described by Sickenberg as a "new" ursid - Bosdagius felinus, is most probably a hyaena milktooth). Although quite rich in forms, the fauna of Volaks does not contain that many significant species to characterize more precise biostratigraphic boundaries and to determine exactly the fauna's age as Middle or Late Villafranchian. KOUFOS & KOSTOPOILLOS (1993) consider that fauna as Mid/Late Villafranchian one. In the later papers of these authors (KOSTOPOULOS & KOUFOS, 1994; KOSTOPOULOS, 1996; KOSTOPOULOS, 1997; KOUFOS & VLACHOU, 1998), the age is more precisely determined, although with some hesitation - Middle Villafranchian (MNQ17). These authors' reasons for such a conclusion are:

1. The artiodactyls from the two above-mentioned localities are rather similar. This statement also concerns the association *Mitilanotherium-Gallogoral-Nyctereutes*, existing in Dafnero too (i.e. in the Middle Villafranchian), but yet unknown from the Late Villafranchian of Greece;

2. The horse from Volaks appears to be similar to that from Dafnero.

All the cited arguments of the Greak researchers seem logical and acceptable. We could also try to specify the biostratigraphic state of the Volaks locality, noting some more of its faunistic features:

1. It is quite possible that *Gazella* sp. from Volaks is identical with *G. bouvrainae* described from Gerakarou (KOSTOPOULOS, 1996; KOSTOPOULOS & ATHANASSIOU, 1997; KOSTOPOULOS, 1997)(see below the biostratigraphy of that locality). It seems *G. bouvrainae* occurred MNQ17 but also MNQ18.

2. *Mitilanotherium* of SE-Europe is connected with the second half of MNQ17 and with MNQ18-19 (as already noted).

Those circumstances, although unable to determine more emphatically the chronological position of that locality, are nevertheless an indication that it represents a Middle Villafranchian fauna of a transitive, quite late type. Similarly to La Puebla, the locality could be placed at the MNQ17-MNQ18 boundary or immediately before it (Fig. 2).

GERAKAROU (GERAKAROU 1). The macrommal fauna of the locality is rich. The new species *Parastrepsiceros koufosi* (KOSTOPOULOS, 1998) described there is a quite interesting and as it seems relict form. (It would be interesting to investigate the affinities of that form to the E-European-Asian *Caproryx*). The placing of this locality before Seneze (MADE VAN der, 1996) does not seem to correspond to the facts. KOSTOPOULOS & KOUFOS (1994) point out that in the typical for the Middle-Late Villafranchian fauna of Europe *Eucladoceros-Cervus-Croizetocerus* association existing in the locality, the first and the last forms seem to be more evolved than the corresponding ones from Seneze. These authors suggest for the locality an age similar to that of Seneze or between Seneze and Olivola -the last opinion seems to be quite acceptable.

Somewhat later KOSTOPOULOS (1996) studied in details the artiodactyls from the locality, finding a similarity between *Eucladoceros senezensis* and its subspecific form from Seneze, and also between the *Leptobos* from Gerakarou and the forms known from Seneze and from the Early Pleistocene of Italy. This author confirms the statement made above that Gerakarou is situated in the late MNQ18: sensu KOSTOPOULOS (1996) this is the time between Seneze and Olivola. This biostratigraphic state is underlined once again in the latest paper of KOUFOS & KOSTOPOULOS (1997).

There are reasons for a further support of this thesis on the base of the data from Slivnitsa and the biostratigraphic statements already expressed in the present work:

1. The carnivores from Gerakarou show a great similarity to those from Slivnitsa (i.e. to the C. St. Giacomo Unit level): Two species of Canis (as probably in Slivnitsa?) - Canis etruscus, C. arnensis and also Panthera gombaszoegensis are presented in the Greek locality (KOUFOS, 1987; 1992; KOUFOS et al., 1995). It was already mentioned above that this carnivore association is being connected with the time of the migrations from the East towards Europe typical for the Plio-Pleistocene boundary. Thus, this is an association typical for the Pleistocene beginning and the Early Pleistocene, which was considered so far not earlier than the Olivola unit. A statement was proposed in this paper that in the Mediterranean (especially the eastern ?) of Europe this group of species enters as early as the C. St. Giacomo unit (incl. Slivnitsa) (see above). Broadly accepted is the opinion that C. arnensis (presented in Gerakarou together with C. etruscus) appears in Europe later (in the Tasso unit) than C. etruscus. Maybe this does not correspond to the reality because C. "senezensis" from Seneze seems to be identical with C. arnensis (see SPASSOV, 1998). We have to note that in Slivnitsa (where fragmentary remains of *C. etruscus* are presented) there are also single finds dimensionally resembling C. arnensis. However, the Pachycrocuta brevirostris occurring in Gerakarou is absent in Slivnitsa which could turn to be one of the main differences here, bearing in mind that this species is a marker of the Olivola unit (i.e. of the boundary MNQ18-a/MNQ18-b: in Europe see Fig. 1-2).

2. The horse from Gerakarou and that from Slivnitsa show a number of common features. Anyway, the two populations are not identical and it seems that this similarity is not a result of a very close phylogenetic relationship, but rather of a similar level of development; it suggests a probable relative proximity in chronological aspect.

3. The two localities are similar also in the great abundance of *Bovidae*, what in fact is typical for the time after St.-Vallier unit. The taxonomic composition of the

bovid fauna and of the artiodactyls as a whole is on the other hand quite different (see in Gerakarou - *Leptobos* cf. *etruscus*, *Leptobos* sp., Gazella bouvrainae, *Parastrepsiceross koufosi*, and also *Sus strozzi*: KOSTOPOULOS, 1996; 1998).

Having in mind all these faunistic peculiarities and especially the presence of *Pachycrocuta brevirostris* in Gerakarou we could suggest that the age of this locality is somewhat later than the age of Slivnitsa - probably corresponding to the boundary between Costa St. Giacomo unit and Olivola unit. After our MNQ zones deffinition the Greek locality of Gerakarou could be placed just in the beginning of MNQ18-b (before Olivola), or on the MNQ18-a2-MNQ18-b boundary (Fig. 2).

APOLLONIA 1. This locality deserves a special interest from the aspect of the study and characterization of the Final-Villafranchian faunas (the End of Early Pleistocene) and the boundary with the Middle Pleistocene ones. The locality is of a special interest also because of its zoogeographic position - in a zone of migrations from the East. The very rich and specific fauna of the locality and its biostratigraphic status are an object of analysis in the last years. Especially characteristic and indicative forms are *Canis apollonensis* Koufos & Kostopoulos. 1997. Meles dimitrius, "Baranogale cf. helbingi", Megantereon megantereon. Bison (Eobison) sp., Praeovibos sp., Pontoceros ambiguus mediterraneus Kostopoulos, 1996, Soeraelia briaittae Kostopoulos, 1996, Caprinae gen, sp. indet. - most probably migrants from Asia, (The Caprinae indet have elongated limb bones and Ovis-like phallangs and it is possibly an Ovis species (?) - person. observations in the Coll. Of the Univ. of Thessaloniki). This fauna is considered as representative for the latest Villafranchian in SE-Europe, probably similar in age to Venta Micena (Spain), as well as to Farneta (Italy), and also corresponding to the MNQ20 zone (Koufos & Kostopoulos, 1994; 1997; 1997a; Koufos et al., 1995; KOSTOPOULOS, 1996; KOSTOPOULOS, in print). (It should also be noted that here is meant the classic concept of Farneta Unit's position; see TORRE et al. 1992; after this concept Pirro is included in the Farneta Unit. In the new paper by GLIOZZI et al. (1997) Pirro is considered a separate, later unit).

In Apollonia's fauna, some of the earliest finds of several genera in Europe are discovered - as especially *Bison (Eobison)* sp., and also relict populations from some genera like *Megantereon* for example. The latter genus is considered to have already disappeared in the central parts of the continent in the very beginning of Pleistocene (WOLSAN, 1993). In the Early Pleistocene this genus is obviously rare in Europe, and only in the Mediterranean it survives until the end of the Early Pleistocene. It seems the latest finds are known from Cueva Victoria (Spain), Farneta to Pirro Unit and, obviously, Apollonia (TURNER, 1992; KOUFOS et al., 1995; GLIOZZI et al., 1997). Typical local forms in Apollonia are the characteristic and very large "Baranogale" and the new species *Canis apollonensis*. Especially interesting is the discovering of forms, typical for the North and the East Pontic region (e.g. *Pontoceros ambiguus*), suggesting most probably an Asia Minor influence. This bovid was described after materials from the Early/Middle Pleistocene deposits (layers with Late Odessian - Psecupian, Tamanian and Tiraspolian types of faunas) from the North Pontic region and Georgia (VERESHCHAGIN et al., 1971). It seems this form had its maximal distribution in the Late Apsheron - the Tamanian complex (ALEKSEEVA, 1984), which should probably correspond to the Farneta unit (in its classic definition) or to the Pirro Unit sensu GLIOZZI et al. (1997). This is the exact period when the invasion of *Pontoceros* on the Balkans should be expected - as is the case with Apollonia.

The coexistence of *Bison* and *Megantereon* shows that the remains of the mentioned artiodactyls are quite early. This is an indication that the time of Apollonia is restricted in rather narrow limits, and earlier then Jaramillo. This circumstance shows once again the similarity to Farneta Unit (in its classic definition - nota mea), which is stressed by the above-cited Greak authors; or with the Pirro Unit sensu GLIOZZI et al. (1997): In Pirro Unit were found the earliest certain *Bison (Eobison)* and the last *Megantereon megantereon* remains (GLIOZZI et al., 1997) in Europe.

As for Venta Micena, the age similarity is more controversial in spite of faunal resemblance. The Spanish locality represents a number of specific faunistic elements maybe connected with the isolated geographic position. The "*Capra*" of that locality is a *Hemitragus* in fact, a genus appearing in Europe earlier than *Capra*, and the form determined as *Bison* needs some additional taxonomical investigation (E. Cregut, M.H.N. - Avignon, pers. communication). Indeed, V. Micena is usually placed on the level of the Farneta unit, but the *Equus granatensis* described from there suggests a probably earlier period of time (EISENMANN, 1955).

As for the MNQ20 zone where Apollonia is situated, GUERIN (1982) places the zone in the beginning of the Middle Pleistocene and in the time after 1 Ma. This determination and the more recent data defining the phenomena typical for Farneta unit (the earliest *Megaceros* in Europe for example), contain a contradiction. A revision is needed of the notions about the time and the limits of the zone which should be placed in the beginning of Middle Pleistocene in connection with the new data. Also needed is a synchronization of the two biochronologic systems (Units and MNQ-zones) after the faunistic associations at the Early/Middle Pleistocene boundary. We could assume that Apollonia is situated in the MNQ20 only if placing that zone (or its beginning at least) before the beginning of the Middle Pleistocene - i.e. in the final Villafranchian faunal associations. In the second part - the end of this MNQ zone we could place the so-called transitive Villafranchian-Gallerian faunal associations (Vallonet) (Fig. 2).

Putting aside the complicated problem of the place of the MNQ20 zone, we could accept the following statement: Apollonia indeed represents the latest European Villafranchian associations, which demonstrate the connection between the East European and the Asian fauna. This locality could be referred

to the end of Farneta unit or above all to Pirro Unit (sensu GLIOZZI et al., 1997): an age similar to or somewhat earlier than the age of Sandalja 1 (Fig. 2).

III. Paleozoogeography and migrations

III. 1. Migratory waves from Asia to Europe in the Late Pliocene after the Varshets and Slivnitsa data

The faunas of Varshets and Slivnitsa, as well as of some other localities on the Balkan Peninsula (e.g. Gerakarou, Apollonia) bring marks of evident similarity with the Mediterranean (S-European) localities of that time, showing at the same time faunal elements obviously related to migrations from the East into Europe (see the Chapter "Palaeozoogeographical features"). The specific geographic position of Bulgaria (and the Balkans in general) are the reason of finding there all the signs of a transitive zone for the migrations of plant and animal species and humans as well. Evidence of the role of those lands as a bridge of spreading (mostly from the East to the West) exists since most ancient geological times. The regions of the Balkans and Asia Minor have played the role of a terrestrial communication more than once, thus enabling the exchange of species between Europe, Asia and Africa.

As we have already seen, the data of appearance and distribution of certain species have most often been connected with the limits of different biochronological units. Such dispersals are biotic events most often marking evident changes of the environment.

The locality of Varshets and the migrants from Asia

Two facts concerning the locality's fauna are of a special interest from the aspect of the dispersal of species from the East:

1. The discovery of *Nyctereutes* cf. *tingi* - a species probably of Central Asian origin; 2. The earliest finds of *Megalovis*, which origin is probably connected with the Central Asian plateaus.

The partial spreading of these species in Europe (this might also concern the new very small species of *Baranogale*) is connected with the Asian influence on that fauna (see also the Chapter "Palaeozoogeographical features of the fauna").

The find of the rather scanty and enigmatic fossil we have determined as *Gazellospira* sp. - a metatarsus from Varshets and another in the probably earlier locality of Roccaneyra (SPASSOV & CREGUT-BONNOURE, 1999) could also be connected with migrations along the Mediterranean in the beginning of the Middle Villafranchian. The clarification of this problem needs more complete finds.

The Slivnitsa locality and the early migration of *Canis, Panthera* and some bovids

It was already mentioned that some faunistic phenomena considered to be typical for the beginning of Pleistocene (mass migrations toward Europe), have started in fact (after the data from Slivnitsa and their connection with some other localities) as far back as in the End of Pliocene.

The appearance of *Canis* s.str. in Europe., The so called "Canis event" (AZZAROLI, 1983; BONIFAY, 1990; MASINI & TORRE, 1990; TURNER, 1992) is connected with the Asian invasion of coyote/wolf-like Canis. The earliest indications of such an invasion come from Costa S. Giacomo (and Seneze if the locality is of Pre-Olduvai age); Here is necessary to note the only something later locality of Gerakarou (KOUFOS, 1992), where two species of *Canis* exist (as probably in Slivnitsa?). The most apparent traces of the "*Canis event*" have been established somewhat later, in the time of the Olivola unit (*C. etruscus*), i.e. at the Plio-Pleistocene boundary (TORRE et al., 1992; ROOK & TORRE, 1996).

The insufficiently studied and earlier than the Late Viillafranchian *Canis*-like forms from Europe are in fact recently separated from *Canis* s.str. (TEDFORD & QIU, 1996). Indeed, KURTEN & CRUSAFONT (1977) have noted the presence of a true *Canis (C. falconeri)* from a time earlier than the C. st. Giacomo unit - in P. de Valverde (MNQ17): one upper P3 and several other tooth fragments. MASINI & TORRE (1990), followed by ROOK (1994), however, express certain doubts about these remains belonging to *C. falconeri*. We also suppose that the remains have been wrongly determined and their taxonomical status should be reviewed. The tooth supposed to be an upper P3, could be in fact determined as a lower P4 after the following features: strongly enlarged hind part of the tooth, and presence of a facette of occlusion on the linguo-distal surface of the tooth's crown base.

It should also be noted that the stratigraphic position of this find from Costa S. Giacomo is not absolutely sure (earlier than Olivola Unit ?), so that it might turn to be not earlier than Olivola.

Having in mind the stratigraphical problems on the age of the *Canis* find from Costa S. Giacomo and Seneze we can appreciate the discovery of *Canis* ex gr. *etruscus* in Slivnitsa as a fact of considerable importance SPASSOV (1998). This locality proposes, most probably, the earliest registration in Europe of the Late Villafranchian "*Canis event*". It, at the same time, appears to confirm the Late Pliocene and not Early Pleistocene age of the penetration of the first wolf-like primitive forms in Europe from the East. On the basis of the material from Slivnitsa, Seneze, C. S. Giacomo and Gerakarou we can suggest that statement as valid for South Europe at least. (In the fauna of the Hapry Complex - near the Sea of Azov with a supposed age the beginning of MNQ17, *Canis etruscus - arnensis* was also announced recently (SOTNIKOVA et al., 1998). As already mentioned above, this could be resulted from the existence of younger layers besides the direct contact with Asia.) **The** *Panthera* **invasion.** In Slivnitsa we note the earliest presence of *Panthera gombaszoegensis* and thus of *Panthera* s.str. as a whole (SPASSOV, 1997a; 1998). *P. gombaszoegensis* has been recorded in Tegelen (2,2-1,7 Ma), but it originates from the uppermost levels there (TURNER, 1992). The earliest true finds of this predator so far seem to be the ones from Gerakarou, Greece (KOUFOS, 1992; KOUFOS et al., 1995) and Olivola, Italy (the Plio-Pleistocene boundary) (TORRE et al., 1992; TURNER, 1992)). The Gerakarou locality should be dated from the Seneze-Olivola units boundary (see above).

The early mass boyidae migrations. The progress of a number of boyids and their invasion from Asia into East Europe and over the whole continent started during the Villafranchian, with the increase of the aridification. Two unknown boyids (not determined up to genus and species) and an Ovis sp. are established in Slivnitsa. The two *Bovidae* spp. (indet.) seem to have no analogue in the other European faunas known so far and, together with the first indication of "Ovis" in Europe mentioned above, could be considered as a testimony of the process of enlarging the areas of Asian species at that time. It was already mentioned that an enigmatic skull of a large Ovis sp. has been determined by Schaub from Seneze and this could be used as another argument of the same dispersal. A strong influence on the migrations from East of the Villafranchian fauna of boyids in Greece is noted by KOSTOPOULOS (1996). It is obvious in the Final Villafranchian locality of Apollonia. In the Greek locality of Gerakarou, which is slightly earlier than Slivnitsa, there too appear some bovids with a taxonomy not clear enough, such as the enigmatic Parastrepsiceros koufosi (KOSTOPOULOS, 1998). (These forms can, most probably, be considered elements from a more Eastern, untypical for W-Europe fauna, expanding its area during the aridification in the SCT10 of ZUBAKOV & BORZENKOVA (1990)). There is no doubt that a more detailed comparison of the so far taxonomically undetermined forms from Slivnitsa and Gerakarou should be of great value.

Climate and migrations. There is some data that in the time corresponding to the Meria cooling (Fig. 1) some Anatolian coastal islands were connected with Asia and that the Black Sea waters were freshened (ZUBAKOV & BORZENKOVA, 1990; DERMITZAKIS, 1990). This suggests a temporary closing of the Bosphorus. The following faunal contact with Asia Minor proposes an explanation of the presence in Slivnitsa of remains of most early migrants (betwen2 - 1,9 Ma.) from the East, e.g. Canis s.str., *P. gombaszoegensis* and a number of *Caprinae*. By the Balkan migratory way they quickly spread in Europe (mainly in the Mediterranean area, where climate and landscapes are similar - Olivola, Seneze).

After removing geographical barriers (e.g. the Bosporus), the migratory waves usually spread instantly from a geological point of view when the new territories grant the same natural conditions as those native for the migrants. Apparently the rate of the mentioned migrations was in Europe high enough after the age of all the Eastern and the Western finds of the earliest migrants. The local conditions, however, could somewhat slow down the tempo of penetration. For instance, the find of *P. gombaszoegensis* in Slivnitsa makes us suppose that some migratory events from the East could possibly be registered in Eastern or SE-Europe somewhat earlier than in the Western or the Central parts of the continent (SPASSOV, 1997a; BOEUF et al., 1997).

III. 2. Palaeozoogeographic characters of the Middle and Late Villafranchian fauna of S.-E. Europe on the examples of Varshets and Slivnitsa

A number of indexes have been created for an easier comparison of the differences and the similarities between the faunas. Useful when comparing fossil mammal faunas from different localities are, for example, E. Simpson's index of resemblance and M. Pickford's index of faunistic distance (when the number of species and individuals/number of bones is great enough (De BONIS et al., 1994)), When determining the appearance of faunas relatively late in geological aspect. such as the Villafranchian ones, the comparison of the geographical affinities of relatively close localities is not so important because they are often evident: The distribution, the origin of species and the natural environment typical for them, are more clear. In this case (similar to the modern faunas) the comparison of entire regions with each other is rather important. Moreover, in such a case it is not enough to search for generic similarities when looking for affinities and differences in such faunas, but the necessity of comparisons on specific, or even subspecific level becomes even more obvious. This, on its turn, makes the use of zoogeographic boundaries and indexes somewhat risky. The determination of the fossil faunas on a level lower than generic is often quite uncertain; data about the distribution of different forms is still insufficient: in such circumstances the affinities between the faunas from different localities could be a result of taphonomic and ecologic, rather than zoogeographic reasons. Of importance in these cases is the determination of the fauna's general appearance after the influence and presence of the concrete species, as far as their distribution areas and origin could be defined at all.

The available data on the distribution of the different taxa, as well as on their adaptive abilities, makes possible to determine more or less their areas of distribution and in a number of cases to suggest their centres of origin as well. Such analyses applied to the species from Varshets and Slivnitsa are useful for the characterization of the zoogeographic appearance of the faunas present in those two localities (Fig. 3-4).

Summarizing the ideas presented in fig 3-4, we could divide the taxa in several groups after their distribution. Those groups make possible a zoogeographic analysis of the Varshets and Slivnitsa faunas. At the same time these groups, as

far as they concern a great number of typical Villafranchian species give information about the zoogeographic relations between the faunas of different regions of Europe and the adjacent territories. They reflect the climatic zones, environment and geographical centres of origin of that time. The taxa from the localities could be divided (some of them not without hesitation, due to the uncertain determination) in the following groups after their distribution:

1. Middle/East European and European (in general) species (it is quite probable many of them are Eurasian forms). Species of that type of distribution are probably adapted to some more "boreal" conditions compared to the typically Mediterranean species, in spite of the fact that the conditions in the Late Pliocene do not seem to show such an expressed zonality as it is in the present days.

2. Eurasian species, distributed mainly in the area known today as Palaearctics (incl. N-Africa). It should be noted that here prevail species, which seem to be typical by this time for the more southern parts of that territory.

3. Species of S-European (Mediterranean) - Fore/Central Asian type of distribution. Species of Circumpontical distribution are also placed here. It is possible indeed future investigations will show that some of these species might be only S-European (Mediterranean endemics) and should not be allied to the Foreasian ones. (A pure European distribution is possible also for some of the species considered here as "Eurasian"). Nevertheless, this is scarcely possible for most of them, bearing in mind the mobility of big mammals. It seems that a number of them are species which have penetrated from the more or less arid areas of Central and Fore Asia into similar landscapes of the N-Pontic region, the Balkans and the European part of the Mediterranean.

Depending on their adaptation to the climatic conditions and, above all, to the humidity, a number of species from Central Asia penetrated also in later times, during the whole Quaternary in certain regions of Europe, using one of the two (sometimes maybe both ?) migratory roads:

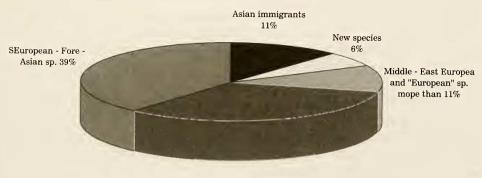
a). The road along the Northern Pontic region (mainly steppe species, resistant to harsher conditions), leading mainly to Eastern-Central Europe.

b). Asia Minor-Balkan road (during a closing of the Bosporus) mainly to the European part of the Mediterranean. It seems that in both cases the Balkans have been influenced by such penetrations.

4. Asian elements (Migrants). Here are concerned species which have reached Europe at some level of their expansion, becoming European species, too. The concept "Asian migrants" could be used here to indicate those species, which are met for a first or nearly first time on the continent in localities like Varshets and Slivnitsa (on the "front line" in Europe) (see also the Chapter: Migratory waves toward Europe in the End of Pliocene).

5. New species: Of course, this is not a zoogeographic category and it is used here quite free, as far as we could only suppose and not decide for sure what these species are after their origin or at least after their distribution.

No. of zoogeographic group after taxa distribution (see the text)	Таха	Distribution after current data
3	Vulpes alopecoides	The European Mediterranean; South Europe
4	Nyctereutes cf. tingi	Central Asia - asian element
2	Ursus minimus - etruscus	Eurasia
1	Martes wenzensiss -	Central Europe
	Martes vetus	(Europe as a whole)
3	Pannonictis ardea	Europe; Fore Asia; Transcaucasia
1	Vormela petenyii	central and East Europe
5	Baranogale nov. sp.	The Balkan Peninsula
3	Meles thorali	South Europe; Fore Asia;
		Transcaucasia
2	Pliocrocuta perrieri	Europe; Central Asia;
		North Africa
2	Lynx issiodorensis issiodorensis	Europe; Asia; ?Africa
3	aff. Viretailurus shaubi	Western Europe; The European Mediterranean
2	Acinonyx pardinensis	South Europe; Central Asia
3	cf. Cervus philisi	Southern and Western Europe
2	Cervidae gen.	Southern and Eastern Europe; ?Asia
1	Eucladoceros senezensis cf. vireti	Southern (Western?) Europe (Europe as a whole?)
3	Gazellospira sp.	Southern Europe
4	Megalovis aff. latifrons	(Europe, Asia) - asian element
3	Equus stenonis cf. vireti	Southern (and Eastern?) Europe



Eurasian ca. 33%

Fig. 3. Geographic area of distribution of the taxa from Varshets

VARSHETS (Fig. 3). Unlike most of the well known Mediterranean faunas, that of Varshets shows a connection with the faunal associations of Middle- and E-Europe; examples supporting that suggestion are forms as *Vormela* (*Pliovormela*) petenyii and Martes wenzensis - vetus; Martes sp. has been found in Italy (see De GIULI et al., 1990) but this genus seems to be rare in the South and the specific belonging still remains unclear). However, the appearance of the fauna of Varshets shows greatest similarity to that of the European-Mediterranean localities. The relationship to Fore Asia is evidently strong, too. In spite of some hindering relativity by the determination of some species, a tendency of prevalence emerges of taxa with S-European and Fore Asian distribution. This, in fact, appears to be quite logical bearing in mind the geographical position of the locality and the clear indications of an influence of Asian elements.

SLIVNITSA (Fig. 4). In its main zoogeographic affinities, the fauna of Slivnitsa follows the same patterns as the earlier fauna of Varshets does. The S-European and Foreasian forms, together with the influence of the first waves of migrants from Asia (see below), are playing an especially important role in creating the general appearance of the faunal complex of the locality. After the fauna of the Slivnitsa locality we could trace the migratory route of the first immigrants from the East, such as *Canis* and *Panthera*, which some later - in the Beginning of Pleistocene - become an important element of the general appearance of the European fauna.

The strong Asian influence on the Balkan fauna could be traced also by the presence of other forms, as *Ovis* sp. and some unidentified bovids, most likely migrants from the East. The data on the Late Villafranchian fauna of Greece and Romania also confirms the strong influence of faunal elements formed most probably in the Fore/Central Asian and East European open spaces: the presence of such genera as *Mitilanotherium*, *Parastrepsiceros*, *Pontoceros* (see the chapter: Biochronology of S-E Europe).

Some authors consider the Late Miocene faunas of Greece and Turkey as belonging to the same zoogeographic region - "Greek-Iranian province", spread from Macedonia to Iran, and probably Afghanistan (De Bonis et al., 1994). Perhaps it would be more correct to call that province Balkan-Iranoturanian including the Northern Pontic area. Thus it would reflect the distribution of the typical "hipparion fauna" of the East European-Foreasian open spaces, which seems to have been quite homogenous.

The distribution and "physiognomy" of the faunas in the end of Pliocene cannot, of course, be similar to those from the end of Miocene. Therefore it would be too risky to express some more concrete suggestions about the abovementioned province in those times. However, the new wave of aridification and the new periodical appearance of a "landbridge" between Asia Minor and the

after taxa distribution (see the text)4Canis ex. gr. etruscusAsian migrant3Vulpes cf. alopecoidesEuropean Mediterranean (S. Europe)3Meles thoraliS. Europe)3Meles thoraliS. Europe)3Meles thoraliS. Europe)2Lutrinae gen.Eurasia, Africa2Hyaenidae gen.Eurasia (recent Palaearctic region)4Panthera cf.Asian migrant gombaszoegensis2Homotherium crenatidensEurope, Central Asia3"Cervus" philisi - Nama" nestiS. and E. Europe1Eucladoceruros cf. tornicornisS. Europe (Europe as a whole?) tornicornis2Gazellospira cf. brivåtenseEurasia (recent Palaearctic region)1Procamptoceras cf. tornicornisEurope3Gallogoral menenghinii phiniiSouth Europe3Gallogoral menenghinii to Asian migrantSouth Europe3Gallogoral sp.Eurasia (recent Palaearctic region)2Megalovis sp.Eurasia (recent Palaearctic region)3Gallogoral menenghinii brivatenseSouth Europe3Gallogoral menenghinii tanseSouth Europe4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-I Asian North Pontic migrant4Bovidae gen. et. sp. indet-II Asian / North Pontic migrant	No. of zoogeographic group	Taxa	Distribution after current data
4Canis ex. gr. etruscus Vulpes cf. alopecoidesAsian migrant European Mediterranean (S. Europe)3Meles thoraliS. Europe, Fore Asia, Transcaucasia2Lutrinae gen.Eurasia, Africa2Hyaenidae gen.Eurasia (recent Palaearctic region)4Panthera cf. gombaszoegensisAsian migrant Europe, Central Asia3"Cervus" philisi - Dama" nestiS. Europe (Europe as a whole?) tornicornis1?Eucladoceruros cf. tornicornisS. Europe Europe2Gazellospira cf. brivatense brivatenseSouth Europe (recent Palaearctic region)1Procamptoceras cf. brivatenseEurope (resent Palaearctic region)1Procamptoceras cf. brivatenseEurope (recent Palaearctic region)2Megalovis sp.Europe (resent Palaearctic region)3Gallogoral menenghinii Pliotragus cf. ardeusSouth Europe Europe (as a whole?)2Megalovis sp.Eurasia (recent Palaearctic region)3Gallogoral menenghinii Heinitragus sp. nov.South Europe Asian migrant4Ovis sp.Asian migrant4Bovidae gen, et. sp. indet-II Asian/ North Pontic migrant4Bovidae gen, et. sp. indet-II Asian/ North Pontic migrant	after taxa distribution		
3Vulpes cf. alopecoidesEuropean Mediterranean (S. Europe)3Meles thoraliS. Europe, Fore Asia, Transcaucasia2Lutrinae gen.Eurasia, Africa2Hyaenidae gen.Eurasia (recent Palaearctic region)4Panthera cf. gombaszoegensisAsian migrant gombaszoegensis2Homotherium crenatidensEurope, Central Asia3"Cervus" philisi - "Dama" nestiS. Europe (Europe as a whole?) tornicornis2Gaellospira cf. brivatenseEurope3Gallogoral menenghinii Pliotragus cf. ardeusSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia (recent Palaearctic region)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-I Asian / North Pontic migrant4Bovidae gen. et. sp. indet-II Asian / North Pontic migrant	(see the text)		
3Meles thorali(S. Europe)3Meles thoraliS. Europe, Fore Asia, Transcaucasia2Lutrinae gen.Eurasia, Africa2Hyaenidae gen.Eurasia (recent Palaearctic region)4Panthera cf.Asian migrant gombaszoegensis2Homotherium crenatidensEurope, Central Asia3"Cervus" philisi - "Dama" nestiS. and E. Europe1?Eucladoceruros cf. tornicornisS. Europe (Europe as a whole?) tornicornis2Gazellospira cf. brivatenseEurasia (recent Palaearctic region)1Procamptoceras cf. brivatenseEurope3Gallogoral menenghinii FivatenseSouth Europe3Gallogoral menenghinii Asian migrantSouth Europe4Ovis sp.Eurasia (recent Palaearctic region)4Ovis sp.Asian migrant4Bovidae gen, et. sp. indet-I Asian/ North Pontic migrant4Bovidae gen, et. sp. indet-II Asian/ North Pontic migrant	4	Canis ex. gr. etruscus	Asian migrant
3Meles thoraliS. Europe, Fore Asia, Transcaucasia2Lutrinae gen.Eurasia, Africa2Hyaenidae gen.Eurasia (recent Palaearctic region)4Panthera cf. gombaszoegensisAsian migrant gombaszoegensis2Homotherium crenatidens "Dama" nestiEurope, Central Asia S. and E. Europe "Dama" nesti1?Eucladoceruros cf. tornicornisS. Europe (Europe as a whole?) tornicornis2Gazellospira cf. brivatense brivatenseEurope3Gallogoral menenghinii Pilotragus cf. ardeusSouth Europe1Pilotragus cf. ardeus Europe (as a whole?)2Megalovis sp. Eurasia Furdagus sp. nov.Eurasia new species (for the moment on the Balkans)4Ovis sp. Asian migrantAsian Morth Pontic migrant4Bovidae gen. et. sp. indet-II Asian / North Pontic migrant	3	Vulpes cf. alopecoides	European Mediterranean
Image: Second			(S. Europe)
2Lutrinae gen.Eurasia, Africa2Hyaenidae gen.Eurasia (recent Palaearctic region)4Panthera cf.Asian migrantgombaszoegensisEurope, Central Asia3"Cervus" philisi - "Dama" nestiS. and E. Europe "Dama" nesti1?Eucladoceruros cf. tornicornisS. Europe (Europe as a whole?) tornicornis2Gazellospira cf. brivåtenseEurasia (recent Palaearctic region)1Procamptoceras cf. brivatenseEurope3Gallogoral menenghinii brivatenseSouth Europe3Gallogoral menenghinii brivatenseSouth Europe5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-I Asian / North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian / North Pontic migrant	3	Meles thorali	S. Europe, Fore Asia,
2Hyaenidae gen.Eurasia (recent Palaearctic region)4Panthera cf.Asian migrant gombaszoegensis2Homotherium crenatidensEurope, Central Asia3"Cervus" philisi - "Dama" nestiS. and E. Europe "Dama" nesti1?Eucladoceruros cf. tornicornisS. Europe (Europe as a whole?) tornicornis2Gazellospira cf. brivatenseEurasia (recent Palaearctic region)1Procamptoceras cf. brivatenseEurope3Gallogoral menenghinii EurasiaSouth Europe1Pliotragus cf. ardeus Europe (as a whole?)2Megalovis sp.Eurasia4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-I Asian / North Pontic migrant			Transcaucasia
2Injection gen4Panthera cf. gombaszoegensis2Homotherium crenatidens2Homotherium crenatidens3"Cervus" philisi - "Dama" nesti1?Eucladoceruros cf. tornicornis2Gazellospira cf. brivåtense2Gazellospira cf. brivåtense3Gallogoral menenghinii1Procamptoceras cf. brivatense3Gallogoral menenghinii1Pliotragus cf. ardeus2Megalovis sp.2Eurasia brivatense3Galloyis sp.4Ovis sp.4Bovidae gen. et. sp. indet-I4Bovidae gen. et. sp. indet-II4Bovidae gen. et. sp. indet-II	2	Lutrinae gen.	Eurasia, Africa
4Panthera cf.Asian migrantgombaszoegensisgombaszoegensis2Homotherium crenatidensEurope, Central Asia3"Cervus" philisi -S. and E. Europe"Dama" nesti"S. and E. Europe1?Eucladoceruros cf.S. Europe (Europe as a whole?)tornicornistornicornis2Gazellospira cf. brivatenseEurasia(recent Palaearctic region)region)tornivatense1Procamptoceras cf.Europebrivatensesouth Europe3Gallogoral menenghiniiSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant	2	Hyaenidae gen.	Eurasia
gombaszoegensis2Homotherium crenatidensEurope, Central Asia3"Cervus" philisi -S. and E. Europe3"Dama" nesti1?Eucladoceruros cf.S. Europe (Europe as a whole?)tornicornisGazellospira cf. brivatenseEurasia2Gazellospira cf. brivatenseEurope3Gallogoral menenghiniiSouth Europe1Procamptoceras cf.Europe5Hemitragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant			(recent Palaearctic region)
2Homotherium crenatidensEurope, Central Asia3"Cervus" philisi - "Dama" nestiS. and E. Europe1?Eucladoceruros cf. tornicornisS. Europe (Europe as a whole?) tornicornis2Gazellospira cf. brivåtenseEurasia (recent Palaearctic region)1Procamptoceras cf. brivatenseEurope3Gallogoral menenghiniiSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant	4	Panthera cf.	Asian migrant
2Inc.S. and E. Europe3"Cervus" philisi - "Dama" nestiS. and E. Europe1?Eucladoceruros cf. tornicornisS. Europe (Europe as a whole?) tornicornis2Gazellospira cf. brivatenseEurasia (recent Palaearctic region)1Procamptoceras cf. brivatenseEurope3Gallogoral menenghiniiSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant		gombaszoegensis	
"Dama" nesti1?Eucladoceruros cf. tornicornisS. Europe (Europe as a whole?) tornicornis2Gazellospira cf. brivåtenseEurasia (recent Palaearctic region)1Procamptoceras cf. brivatenseEurope3Gallogoral menenghiniiSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant	2	Homotherium crenatidens	Europe, Central Asia
1?Eucladoceruros cf. tornicornisS. Europe (Europe as a whole?) tornicornis2Gazellospira cf. brivåtense (recent Palaearctic region)1Procamptoceras cf. brivatense3Gallogoral menenghinii Pliotragus cf. ardeus1Pliotragus cf. ardeus2Megalovis sp.5Hemitragus sp. nov. new species (for the moment on the Balkans)4Ovis sp.4Bovidae gen. et. sp. indet-I Asian / North Pontic migrant4Bovidae gen. et. sp. indet-II Asian / North Pontic migrant	3	"Cervus" philisi -	S. and E. Europe
Image: International constraintsImage: International constraints2Gazellospira cf. brivatenseEurasia (recent Palaearctic region)1Procamptoceras cf. brivatenseEurope3Gallogoral menenghiniiSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian/ North Pontic migrant		"Dama" nesti	
2Gazellospira cf. brivatenseEurasia (recent Palaearctic region)1Procamptoceras cf. brivatenseEurope3Gallogoral menenghiniiSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant	1?	Eucladoceruros cf.	S. Europe (Europe as a whole?)
2Characteristic in an annumber of the		tornicornis	
1Procamptoceras cf. brivatenseEurope3Gallogoral menenghiniiSouth Europe3Gallogoral menenghiniiSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian/ North Pontic migrant	2	Gazellospira cf. brivatense	
brivatense3Gallogoral menenghiniiSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian/ North Pontic migrant			(recent Palaearctic region)
3Gallogoral menenghiniiSouth Europe1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian / North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian / North Pontic migrant	1	Procamptoceras cf.	Europe
1Pliotragus cf. ardeusEurope (as a whole?)2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian/ North Pontic migrant		brivatense	
2Megalovis sp.Eurasia5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian/ North Pontic migrant	3	Gallogoral menenghinii	South Europe
2Integration explicitIntegration explicit5Hemitragus sp. nov.new species (for the moment on the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian/ North Pontic migrant	1	Pliotragus cf. ardeus	Europe (as a whole?)
the Balkans)4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian/ North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian/ North Pontic migrant	2	Megalovis sp.	Eurasia
4Ovis sp.Asian migrant4Bovidae gen. et. sp. indet-IAsian / North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian / North Pontic migrant	5	Hemitragus sp. nov.	new species (for the moment on
4Bovidae gen. et. sp. indet-IAsian / North Pontic migrant4Bovidae gen. et. sp. indet-IIAsian / North Pontic migrant			the Balkans)
4 Bovidae gen. et. sp. indet-II Asian/ North Pontic migrant	4	Ovis sp.	
4 Bovidae gen. et. sp. indet-II Asian/ North Pontic migrant	4		
	4	Bovidae gen. et. sp. indet-II	Asian/ North Pontic migrant
1 Equus cf. stenonis Europe (the Mediterranean?)	1		Europe (the Mediterranean?)

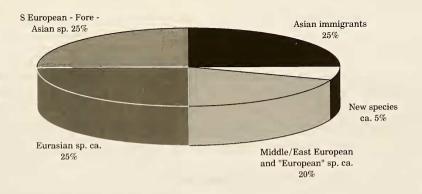


Fig. 4. Geographic area of distribution of the taxa from Slivnitsa



minimum

Fig.5. Right upper P4 of *Vulpes* sp. from Musselievo (second half of MNQ15 - the earliest find of the *Vulpes* genus in Europe) A: occlusial view of the tooth from Musselievo (at right) and left upper P4 of *Vulpes* cf. *alopecoides* from Slivnitsa (beginning of MNQ18) (at left); B: the same teeth - P4 from Musselievo (left) and P4 from Slivnitsa (right) - lingual view; C: the same teeth - P4 from Musselievo (right) and P4 from Slivnitsa (left) - labial view.





Balkans result in the preserving or repeated creation of a number of similarities and connections between the faunas of the above-mentioned regions (see below). At the same time, just like recently - in the forming of the Late Pleistocene and Holocene faunas of the Balkans and Europe, the Asia Minor-Balkan and the North Pontic routes are playing an important role for the penetration of Asian elements in Europe. They reach the Balkans usually via one or the other of the two routes and could penetrate to the West looking for suitable conditions, similar to those they have been formed in.

Acknowledgments

I am very grateful to Dr. D. Kostopoulos (Aristotle Univ. of Thessaloniki, Greece), Dr. C. Guerrin (Univ. of Lyon 1) and Prof. E. Delson (A.M.N.H., New York) for the useful comments on the manuscript and the discussions as well as to Mr. G. Hristov from Pleven who discovered the Musselievo locality and handed the fossil material.

References

AGUIRRE E., J. MORALES. 1990. Villafranchian Record of Spain. - Quartärpaläontologie. Berlin, 8: 7-11.

- AGUSTI J., S. MOYA-SOLA, J. PONS-MOYA. 1987. La sucesion de mammiferos en el Pleistoceno inferior de Europa: Proposicion de una nueva escala biostratigrafica. - Paleont. I Evol., mem. esp. 1. 287-295.
- ALBERDI M., L. CALOI, M. PALOMBO. 1998. Large mammal associations from the Early Pleistocene: Italy and Spain. - The Dawn of Quaternary. Mededelingen Nederlands voor Inst. voor Toegepaste Geowetenschappen, 60: 521-532.
- ALEKSEEVA L. 1984. The Pecularities of the Apsheronian Mammalian Association of East Europe. - In: Antropogen Eurasii. Nauka, Moscow, 180-184. (In Russian).
- AZANZA B., M. ALBERDI, E. SERDENO, J. PRADO. 1997. Biochronology from the Latest Miocene to Middle Pleistocene in the Western Mediterranean area, a multivariate approach. Actes du congres Biochrom' 97. J.-P. Aguilar, S. Legendre & J. Michaux (eds). Mem. Trav. E.P.H.E., Inst. Montpellier, 21: 567-574.
- AZZAROLI A. 1977. The Villafranchian Stage in Italy and the Plio-Pleistocene Boundary. G. Geol. 41 (2): 61-79.
- AZZAROLI A. 1983. Quaternary Mammals and the "End-Villafranchian" Dispersal Event A Turning Point in the History of Eurasia. Palaeogeography, Palaeoclimatology, Palaeoecology. Amsterdam, 44: 117-139.
- BAKSI A. 1993. A geomagnetic polarity time scale for the period 0-17 Ma, based on ⁴⁰ Ar/³⁹ Ar plateau ages for selected field reversals. Geophysical Research letters, **20** (15): 1607-1610.
- BOEUF O. 1997. Chilhac, Seneze, Blassac-La-Gironde (Haute Loire, France), Gisements du Pliocène terminal, géographiquement proches. Leur interêt biochronologique. Biochrom'97 - Montpellier, 14-17 Avril, 1997. Résumés, 31.
- BOEUF O., E. CREGUT, G. KOUFOS, L. FLYNN, J. MICHAUX, C. RADULESCU, N. SPASSOV, E. TERSEA,
 D. TORRE. 1997. Biochronologie du Pliocène. in: J.-P. Aguilar et al. Syntheses et tableaux
 de correlations. Biochrom'97. Congrès International de Biochronologie Mammalienne.
 Mém. Trav. E.P.H.E., Inst. Montpellier, 21: 799-802.
- BOEV Z. 1996. Tertiary Avian Localities in Bulgaria. Acta Univ. Carolinae. Geol., 39: 541-545.
- BOEV Z. 1998. Peafowls (g. *Pavo* Linnaeus, 1758) and Ptarmigans (g. *Lagopus* Brisson, 1760): An unique coexistence in North Bulgaria over 3 m. y. ago. - Biogeographia, Nuova Serie, 19: 219-222.
- BOEV Z. In press. Early Pliocene aviafauna of Musselievo (C Northern Bulgaria) Acta zool. cracoviensia.
- BONIFAY M.-F. 1990. Relations Between Paleoclimatology and Plio-Pleistocene Biosratigraphic Data in West Countries. - In: E. Lindsay et al. (eds). European Neogene Mammal Chronology. Plenum Press, New York.
- BRUIJN H., R. DAAMS, G. DAXNER-HOCK, V. FAHLBUSCH, L. GINSBURG, P. MEIN, J. MORALES. 1992. Report of the RCMNS working group on fossil mammals, Reisenburg 1990. - Newsl. Stratigr. Berlin - Stuttgart, 26 (2/3): 65-118.
- DEBARD E., M. FAURE, C. GUERIN. 1994. Stratigraphie du gisement villafranchien de Saint-Vallier (Drome). C. R. Acad. Sci. Paris, t. 318, ser. II: 1283-1286.
- DE BONIS L., G. BOUVRAIN, D. GERAADS, G. KOUFOS, S. SEN, P. TASSY. 1994. Biochronologie, paleoécologie, et relations paleobiogéographiques. In: Sen S. (Coord.). Les gisements de mammifères du Miocene supérieur de Kemiklitepe, Turquie. Bul. Mus. Nat. d'Hist. Natur., sér. 4, sect. C, 16 (1): 240 p.
- DE GIULI F., MASINI, D. TORRE. 1990. The Latest Villafranchian Faunas in Italy The Pirro Nord local fauna (Apricena, Gargano). - Quartärpaläontologie. Berlin, 8: 29-34.
- DERMITZAKIS M. 1990. The Evolution of the Aegeis during the Late Cenozoic. Geologica Balkanica. Sofia, 20 (3): 3-16.

- DUVERNOIS M.-P., C. GUERIN. 1989. Les Bovidae (Mammalia, Artiodactyla) du Villafranchien Superieur d'Europe Occidentale. - Geobios, 22 (3): 339-379.
- EISENMANN V. 1980. Les chevaux (*Equus* sensu lato) fossiles et actuels: crânes et dents jugales superieures. Cahiers de paleontologie. Ed. du CNRS, 186 p.
- FLYNN J., B. MACFADDEN, M. MACKENA. 1984. Land mammal ages, faunal heterochrony, and temporal resolution in Cenosoic terrestrial sequences. J. Geology, 92: 687-705.
- GINSBURG L. 1998. Le gisement de vertebres pliocenes de Calta, Ankara, Turquie. Carnivores. - In: Plocene vertebrate locality of Calta, Ankara, Turkey. - Geodiversitas, 20 (3): 379-396.
- GAUTIER F., E. HEINTZ. 1974. Le gisement villafranchien de la Puebla de Valverde (Province de Teruel, Espagne). Bull. du Mus. d'Hist. Naturelle, ser. 3, 36 (228): 113-137.
- GLIOZZI E., L. ABBAZZI, P. ARGENTI, A. AZZAROLI, L. CALOI, L. CAPASSO BARBATO, G. DI STEFANO, D. ESU, G. FICCARELLI, O. GIROTTI, T. KOTSAKIS, F. MASINI, P. MAZZA, C. MEZZABOTTA, M. PALOMBO, C. PETRONIO, L. ROOK, B. SALA, R. SARDELLA, E. ZANALDA, D. TORRE. 1997. Biochronology of selected Mammals, Moluscs and Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. Revista Ital. Paleont. Stratigr., 103 (3): 369-388.
- GUERIN C. 1982. Premiere Biozonation du Pleistocene Europeen, principal resultat biostratigraphique de l'etude des Rhinocerotidae du miocene terminal au pleistocene superieur d'Europe Occidentale. - Geobios, 15 (4): 593-598.
- GUERIN C. 1990. Biozones or Mammal Units? Methods and limits in Biochronology. In: Lindsay et al. (eds). European Neogene Mammal Chronology. New York, Plenum Press.
- HEINTZ E. 1970. Les cervides villafranchiens de France et d'Espagne. Voll. I-II. Memoires du Museum National d'Histoire Naturelle, Nouv. Ser., Ser. C, 12:
- HEINTZ E. 1978. La faune villafranchienne de la Puebla de Valverde, Teruel, Espagne. Compositiuon qualitative et quantitative. - Geologie Mediterraneene, 5 (2): 277-280.
- HEINTZ E., C. GUERIN, R. MARTIN, A. PRAT. 1974. Principaux gisements Villafranchiens de France: Listes fauniques et biostratigraphie. - Mem. B.R.G.M., Paris, 78 (1): 170-181.
- JANOSSY D. 1986. Pleistocene vertebrate faunas of Hungary. In: Palaeontology and Stratigraphy, No. 8. Elsevier. Amsterdam-Oxford-New York-Tokyo, 208 p.
- KORMOS T. 1937. Zur Geschichte und Geologie der oberpliozanen Knochenbreccien des Vilklanyer Gebirges. - Math. Term. Tud. Ert., 56: 1061-1110.
- KOSTOPOULOS D. 1996. The Plio-Pleistocene Artiodactyls of Macedonia (Greece). Dissertation thesis, Aristotle Univ. of Thessaloniki, Dept. of Geology, 540 p.
- KOSTOPOULOS D. 1997. The Plio-Pleistocene Artiodactyls from Macedonia, Greece: 2. The fossiliferous Locality of Volakas, VOL (Volakas Basin, Drama, NE Greece). -Paleontologia i Evolutio, 30-31: 83-92.
- KOSTOPOULOS D. 1998. *Parastrepsiceros koufosi* n.sp. (Mammalia: Bovidae); note on the possible presence of a Prostrepsiceros descendant in the latest Pliocene of northern Greece. Acta zool. Cracov. 41 (1): 101-109.
- KOSTOPOULOS D. In press. The Plio-Pleistocene Artiodactyls of Macedonia, (N. Greece): 2. The Fossiliferous Site "Apollonia-1", APL (Mygdonia Basin, Greece). - Bull. Mus. Natl. Hist. Nat., Paris.
- KOSTOPOULOS D., V. ATHANASSIOU. 1997. Les Gazelles du Pliocene moyen-terminal de la Grece continentale (Macedonie, Thessalie). - N. Jb. Geol. Palaont. Abh., **205** (3):413-430.
- KOSTOPOULOS D., G. KOUFOS. 1994. The Plio-Pleistocene artiodactyls of Macedonia (Northern Greece) and their biostratigraphic significance; preliminary report. - C. R. Acad. Sci. Paris, 318 (2): 1267-272.
- KOSTOPOULOS D., G. KOUFOS. 1995. New Considerations about the division of Villafranchian. -Xth RCMNS Congress, Bucharest, September, 1995. - Rom. Journ. of Strat., Abstracts, pp.2.

- KOHFOS G. 1987. *Canis arnensis* Del Campana, 1913 from the Villafranchian (Villanyian) of Macedonia (Greece). Paleontologia i Evolutio, 21: 3-10.
- KOUFOS G. 1992. The Pleistocene carnivores of the Mygdonia Basin (Macedonia, Greece). -Ann. de Paleontol., 78 (4): 205-257.
- KOUFOS G. 1993. Late Pliocene carnivores from western Macedonia (Greece). Palaont. Z., 67 (3/4): 357-376.
- KOUFOS G. 1997. The canids *Eucyon* and *Nyctereutes* from the Ruscinian of Macedonia, Greece. Paleontologia i Evolutio, **30-31**: 39-48.
- KOUFOS G., D. KOSTOPOULOS. 1993. A stenonoid horse (Equidae, Mammalia) from the Villafranchian of Westhern Macedonia (Greece). - Bull. Geol. Soc. Greece, 38 (3): 131-141.
- KOUFOS G., D. KOSTOPOULOS. 1997 Biochronology and succession of the Plio-Pleistocene Macromammalian localities of Greece. In: J.-P. Aguilar, S. Legendre, & J. Michaux (eds). Actes du Congrès Biochrom'97. - Mem. Trav. E.P.H.E., Inst. Montpellier, 21: 619-634
- KOUFOS G., D. KOSTOPOULOS. 1997a. New Carnivore Material from the Plio-Pleistocene of Macedonia (Greece) with the description of a new Canid. - Munchner Geowiss. Abh. 34: 33-63.
- KOUFOS G., D. KOSTOPOULOS, K. KOLIADIMOU. 1991. Un nouveau gisement de mammiferes dans le Villafranchien de Macedonie occidentale (Grece). - Comptes Rendus de l'Acad. Sci. Paris, Ser. II, 313: 831-836.
- KOUFOS G., G. SYDIRES, G. KOSTOPOULOS, K. KOLIADIMOU. 1995. Preliminary results about the stratigraphy and the palaeoenvironment of Mygdonia basin, Macedonia, Greece Geobios, 18: 243-249.
- KRETZOI M. 1956. A Vilanyi-hegyseg also-pleisztozen gerinces-faunai. Geol. Hung., Ser. Palaeont., 27:1-264.
- KURTEN B., M. CRUSAFONT PAIRO. 1977. Villafranchian Carnivores (Mammalia) from La Puebla de Valverde (Teruel, Spain). - Comment. Biol. Soc. Scient. Fennica, Helsinki, Helsingfors, 1-39.
- MALEZ M. 1975. On the Significance of the genus *Homo* discovery in the Villafranchian sediments of Sandalja 1 near Pula. Rad Jugosl. Akad. znanosti i umjetnosti. Razred za prirodne znanosti. Zagreb, **371** (17): 181-201.
- MARTIN R. 1971. Les affinites de *Nyctereutes megiastoides* (Pomel) canide du gisement villafranchien de Saint-Vallier (Drome, France). Palaeovertebrata, 4 (2): 40-58.
- MARTIN R. 1973. Trois nouvelles espèces de Canidae, Carnivora des gisements Plio-Villafranchiens d'Europe. - Doc. Lab. de Geol. de la Fac. des Sci. de Lyon. Notes et Memoirs, **57**: 87-96.
- MASINI F., D. TORRE. 1990. Large mammal dispersal events at the beginning of the Late Villafranchian. in: Lindsay et al. (eds). - European Neogene Mammal Chronology. Plenum Press, New York.
- MAZZA P., M. RUSTIONI. 1994. On the Phylogeny of Eurasian Bears. Palaeontographica Abt. A, Stuttgart, 230 (1-3): 1-38.
- MEIN P. 1975. Résultats du groupe de travail des Vertébrés. Report on activity on the RCMNS working group (1971-1975), IUGS, regional committee on Mediterranean Neogene stratigraphy, 78-81.
- MEIN P. 1990. Updating of MN zones. in: Lindsay et al. (eds). European neogene Mammal Chronology. New York, Plenum Press, 73-90.
- MONTURE S. 1994. Communautés de mammifères et environements: l'apport des faunes aux reconstructions des milieux en Europe depuis le Pliocène et l'impact des changements climatiques sur la diversité. Thèse de doctorat. Acad. de Montpellier. Univ. de Montpellier, 2.

- POPOV V. 1991. Quaternary small mammals (Mammalia, Insectivora, Lagomorpha, Rodentia) from the Western Prebalkan: morphology, paleoecology, biostratigraphy. -Thesis. Inst. of zoology, Bulg. Acad. Sci. Sofia. (in Bulgarian).
- POPOV V., H. DELCHEV. 1997. Formation of the recent fauna. In: Geography of Bulgaria. "Marin Drinov" Acad. Publ. House . Sofia, 310-315. (In Bulgarian).
- QIU ZHANXIANG, R. TEDFORD. 1990. A Pliocene species of Vulpes from Yusche, Shanxi. -Vertebrata Palasiatica, 28 (4): 245-258.
- RADULESCO C., P. SAMSON. 1990. The Plio-Pleistocene Mammalian Succession of the Oltet Valley, Dacic Basin, Romania. Quartarpalaontologie, Berlin, 8: 225-232.
- RADULESCU C., P. SAMSON. 1995. Review of the Villafranchian s.s. faunas of Romania. Il Quaternario, 8 (2): 377-382.
- ROOK L. 1994. The Plio-Pleistocene Old Word Canis (Xenocyon) ex gr. falconeri. Bolletino della Societa Paleontologica Italiana, 33 (1): 71-82.
- ROOK L., D. TORRE. 1996. The wolf-event in the western Europe and the beginning of the Late Villafranchian. N. Jb. Geol. Palaont. Mh., 8: 495-501.
- SCHAUB S. 1944. Die oberpliocaene Saugetierfauna von Seneze (Haute-Loire) und ihre verbreitungsgeschichtliche Stelung. Eclog. Geol. Helvet., Bazel, 21 (1): 260-266.
- SICKENBERG O. 1968. Die Unterpleistozane fauna von Volaks (Griech. Mazedonien). Geol. Jb., 85: 33-54.
- SOTNIKOVA M., V. BAIGUSHEVA, V. TITOV. 1998. Revision of the carnivores from the Haprovsk faunal complex. In: Glavneyshie itogi v izuchenii chetvertichnogo perioda i osnovnie napravlenya issledovaniy v XXI veke. - Abstracts of papers. St. Petersburg.
- SPASSOV N. 1995. Contemporary Development of the Vertebrates Paleontology in Bulgaria. - EUROPAL. Europ. Palaeont. Assoc. Newsletter Lyon, 7: 43-44.
- SPASSOV N. 1997a. Villafranchian Succession of Mammalian Megafaunas from Bulgaria and the Biozonation of South-East Europe. - In: J.-P. Aguilar, S. Legendre, & J. Michaux (eds). Actes du Congres Biochrom'97. Mem. Trav. E.P.H.E., Inst. Montpellier, 21: 669-676.
- SPASSOV N. 1997b. Varshets and Slivnitsa: New Rich Localities of Vertebrate Fauna from Bulgaria (Taxonomical Composition, Biostratigraphy, Climatochronology). - Geologica Balcanica, Sofia.
- SPASSOV N. 1997c. The Villafranchian mammalian fauna and Its investigation in Europe, on the Balkans and in Bulgaria. Geologica Balcanica. Sofia.
- SPASSOV N. 1998. A New Late Villafranchian Locality of Vertebrate Fauna Slivnitsa (Bulgaria) and the Carnivore Dispersal Events in Europe on the Pliocene/Pleistocene Boundary. - Hist. Nat. Bul., 9: 101-113.
- SPASSOV N., E. Cregut-Bonnoure. 1999. First Datas about the Villafranchian Antilopinae and Caprinae of bulgaria: Richness and biogeographical signification. - Comptes rendus Acad. Sci., Paris.
- STEININGER F., R. BERNOR, V. FAHLBUSH. 1990. European Neogene marine/Continental Chronologic Correlations. - In: Lindsey E., V. Fahlbush, P. Mein. (eds). European Neogene Mammal Chronology. New York, Plenum Press, 15-46.
- SZALAY F., E. DELSON. 1979. Evolutionary history of primates. New York etc. Acad. Press, 434 p.
- TCHERNOV E., C. GUERIN. 1986. Conclusions sur la faune du gisement pleistocene ancien d'Oubeidiyeh (Israel): Implicatians paleoecologiques, biogeographiques et stratigraphiques. - In: Les mammiferes du Pleistocene inferieur de la vallee du Jourdain a Oubeidiyeh. Mem. et travaux du centre de recherches francais de Jerusalem, 5: 351-398.
- TEDFORD R., Z. QIU. 1991. Pliocene Nyctereutes (Carnivora: Canidae) fom Yushe, Shanxi, with comments on chinese fossil racoon-dogs. - Vertebrata Palasiatica, 29 (3): 179-189.

- TEDFORD R., Z. QIU. 1996. A New Canid Genus from the Pliocene of Yushe, Shanxi Province. - Vertebrata Palasiatica, 34 (1): 35-49.
- TORRE D., G. FICCARELLI, F. MASINI, L. ROOK, B. SALA. 1992. Mammal Dispersal Events in the Early Pleistocene of Western Europe. - Courier Forsch. Inst. Senckenberg, 153: 51-58.
- TORRE D., A. ALBIANELLI, A. AZZAROLI, G. FICCARELI, M. MAGI, G. NAPOLEONE, M. SAGRI. 1993. Palaeomagnetic Calibration of Late Villafranchian Mammalian Faunas from the Upper Valdarno, Central Italy. - Mem. Soc. Geol. It., 49: 335-344.
- TORRE D., A. ALBIANELLI, A. BERTINI, G. FICCARELLI, F. MASINI, G. NAPOLEONE. 1996. Paleomagnetic calibration of Plio-Pleistocene mammal localities in central Italy. Acta zool. Cracov., 39 (1): 559-570.
- TURNER A. 1992. Villafranchian-Galerian Larger Carnivores of Europe: Dispersions and Extinctions. - In: W. v. Koenigswald, L. Werdelin (eds). Mammalian Migration and Dispersal Events in the European Quarternary. Cour. Forsch. Inst. Senckenberg, 153. Frankfurt a. M., 153: 153-160.
- VANGENHEIM E. 1977. Paleontological justification of the quaternary stratigraphy of North Asia. - Nauka, Moscow, 171 p. (In Russian).
- VAN DER MADE J. 1996. Biogeography of some species of Sus at the dawn of the Quaternary. in: The Dawn of the Quaternary (16-21 June, 1996. Kerkrade - The Netherlands). - Vol. of abstracts. Geol. Survey of The Netherlands RGD, 61 p.
- VERESHCHAGIN N., L. ALEKSEEVA, A. DAVID, V. BAIGUSHEVA. 1971. Pontoceros Verescagin, Alekseeva, David, Baigusheva, gen. nov. - In: K. Nikiforova (ed.). Pleistozen Tiraspolia. STIINZA Publ., Kishinev., 167-169. (In Russian).
- VIRET J. 1954. Le loess a bancs durcis de Saint-Vallier (Drome) et sa faune de mammiferes villafranchiens. Nouv. Arch. Mus. nat. Lyon, 4: 200 p.
- WERDELIN L., A. Turner. 1996. Turnover in the guild of larger carnivores in Eurasia across the Miocene-Pliocene boundary. - Acta zool. Cracov. 39 (1): 585-592.
- WOLSAN M. 1993. Evolution des carnivores quaternaires en Europe Centrale dans leur contexte stratigraphique et paleoclimatique. L'Anthropologie. Paris, 97 (2/3): 203-222.
- ZIJDERVELD J., F. HILGEN, C. LANGEREIS, P. VERHALLEN, W. ZACHARIASSE. 1991. Integrated magnetostratigraphy and biostratigraphy of the upper Pliocene - Lower Pleistocene from the Monte Singa and Crotone areas in Calabria, Italy. - Earth Planet. Sci. Lett., Amsterdam, 107: 697-714.
- ZUBAKOV V., I. BORZENKOVA. 1990. Global Palaeoclimate of the Late Cenozoic. In: Palaeontology and Stratigraphy., Elsevier. Amsterdam, New York, Oxford, Tokyo, 12: 456 p.

Received on 5.1.1999

Author's address: Nikolai Spassov National Museum of Natural History 1, Tsar Osvoboditel Blvd 1000 Sofia, Bulgaria e-mail: wild_fund@mbox.cit.bg

Биохронология и зоогеографски афинитети на вилафранкската фауна от България и Южна Европа

Николай СПАСОВ

(Резюме)

Пърбият повей на смяната на русцинската с билафранкска фауна и на актибното наблизане на степни елементи може да бъде отбелязан на Балканите с находишето Муселиево (втора половина на зона MNQ15). Новите богати български находища Вършец (St. Vallier unit) и Слибница (Costa St. Giacomo unit) представят сукцесия на късноплиоценски фауни и дават основание за сравняване и анализ на оснобните билафранкски находища от Югоизточна Ебропа. Такиба са например Valea Roscai, La Pietris, Valea Graunceanului, Fintinalui Mitilan (Румъния), Sandalja-1 (Хърватска), Dafnero-1, Volaks, Gerakarou, Apollonia (Гърция). Същевременно тезй находища събладат с бремето на бажни миграцонни процеси от изток към Ебропа и показбат първите наблизания на отделни фаунистични елементи 6 сухоземната фауна на континента. Тези миграции са следствие на климатичните промени 6 началото на средния вилфранк и по време на захлаждането Мериа (= SCT10 на Zubakov & Borzenkova). Разпространението на редица видове на запад, особено в Средиземноморската зона е било много бързо поради наличие на подходящи условия. Началото на късния билафранк 6 Ебропа би тряббало да съблада с климатозоната SCT10. със С. St. Giacomo Unit и със зона MNQ18. Същебременно тази зона трябва да бъде дефинирана наново. Тя може да бъде подразделена на MNQ18 - a1; MNQ18-a2 (= C. St. Giacomo Unit) и MNQ18-b (= Olivola Unit). Използването на биохроноложките критерии разработени за запасноебропейския билафранк могат да бъдат прилагани 6 Източна и Югоизточна Ебропа, но като се държи сметка за съществуването на реликтни и локални фауни, како и за азиатското влияние там. В богатите фауни от Вършец и Сливница доминират южноевропейскопредноазиатските бидобе. Тоба гобори бероятно за съществуване на медитеранско-южноебролейско разпространение на редица видове едри бозайници, както и за силното блияние на азиатската фауна върху фауната на Югоизточна Европа, а може би и върху южните части на Европа като цяло.